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VOCALIZATIONS AND BREEDING BEHAVIOR OF ATLANTIC WALRUSES IN THE CANADIAN HIGH ARCTIC

BY

BECKY LYNN SJARE ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

DEPARTMENT OF ZOOLOGY

Edmonton, Alberta

SPRING 1993

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled VOCALIZATIONS AND BREEDING BEHAVIOR OF ATLANTIC WALRUSES IN THE CANADIAN HIGH ARCTIC submitted by BECKY LYNN SJARE in partial fulfilment of the requirements for the degree of DOCTOR OF PHILOSOPHY.

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ABSTRACT

The underwater vocalizations, breeding behavior, distribution, and abundance of Atlantic walruses, *Odobenus rosmarus rosmarus*, overwintering in the Dundas Island polynya (76° 09'N, 94° 52'W) and Penny Strait region of the Canadian High Arctic were studied from 1987 to 1989. Approximately 200 walruses overwinter in this area; 25 to 65 remain in the Dundas Island polynya each winter. Winter distribution of walruses is determined by the presence of open water, areas of thin annual ice, and sea-ice features (e.g., cracks) that allow easy access to open water. The low numbers of walruses and the sedentary nature of the population appear to be important factors influencing their social organization, breeding behavior, and mating system. Walruses breeding in the polynya have a female-defense mating system. Large mature males compete for exclusive access to a herd of walruses containing females and then closely associate with them for one to five days. When attending a herd, a male continuously repeats a complex, stereotyped underwater song. Other sexually mature males in the area behave as silent herd members, vocal satellite males, or, in some cases, both. It is not evident that female preference is important in determining which male becomes the attending male.

Male walruses emit four types of songs - a coda song, a diving vocalization song (DV song), an intermediate song, and an aberrant song. The coda and DV songs are stereotyped and shared by all males in the polynya. Although the basic structure and organization of the coda and DV songs has remained consistent since 1981, their frequency of occurrence varies between years. Intermediate and aberrant songs are not sung by all males and often are not stereotyped. The type and duration of songs emitted by a male are significantly influenced by the social context in which he sings. Singing appears to maintain dominance relationships among males. There is sufficient individual variation in the surface codas emitted by mature males to allow reliable identification, provided that sample sizes and sampling techniques are adequate. Seven of 18 males emitted two distinct types of surface codas; most males varied the structure of their surface coda(s) relative to social context. Generally, these variations did not result in incorrect identification. However, the use of surface codas as individually distinctive vocalizations is limited by the variability in their structure in some circumstances.

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1. GENERAL INTRODUCTION

This thesis examines the breeding behavior, vocal behavior, and distribution and abundance of Atlantic walruses, *Odobenus rosmarus rosmarus*, in the Penny Strait region of the Canadian High Arctic.

1.1 BREEDING BEHAVIOR

The evolution of social behavior and mating systems has been the focus of much research interest ever since Darwin first discussed sexual selection. However, in the last 15 years we have begun to develop a better understanding of how evolutionary forces affect social behavior and have learned more about the long-term social behavior of wild animals (Rubenstein and Wrangham 1986). Both developments emphasize that a diverse range of social behaviors, including mating, could be understood better if individual benefits and the importance of environmental pressures were brought into sharper focus (Rubenstein and Wrangham 1986). Prior to 1977, several studies were successful in providing an ecological understanding of mating systems (Verner 1964; Crook 1965; Verner and Willson 1966; Orians 1969; Selander 1972; Bartholomew 1970; Stirling 1975), but there had been no attempt to synthesize natural history data into a unified theory explaining the evolution of mating systems (Rubenstein and Wrangham 1986). Emlen and Oring (1977) argued that the potential for polygyny was determined by: the relationship between environmental factors and the temporal and spatial distribution of females; whether multiple mates or resources to attract multiple mates were defendable; and whether or not males could capitalize on this potential. Their insights have been accepted as the most comprehensive theory of mating system evolution and have shaped how researchers interpret reproductive behavior within the larger context of social behavior.

Studies on the evolution of social behavior and mating systems in most species of pinnipeds, excluding elephant seals, northern fur seals, and perhaps California sea lions, lag behind those of many other mammal and bird species because of the difficulty of working on species that spends much of their time in the water. Despite the lack of detailed field studies on the social behavior of many species, a reasonably good theoretical understanding of the evolutionary pressures affecting the social behavior of pinnipeds has been achieved. The relationship between sexual dimorphism and polygynous mating systems, and the importance of terrestrial parturition were recognized years ago (Nutting 1891; Bertram 1940), but were not incorporated into a comprehensive model until 1970 with Bartholomew's insightful paper on the evolution of pinniped polygyny. Bartholomew proposed that adaptations for marine feeding and the need for terrestrial parturition were the primary determinants for the evolution of polygyny. His observations on the ecological factors influencing the spatial and temporal distribution of females and on how males capitalize on the opportunity to monopolize multiple mates paralleled all the major components of Emlen and Oring's 1977 model surprisingly well. However, a major shortcoming of Bartholomew's model was that it dealt primarily with the evolution of polygyny in otariids and elephant seals, but with none of the remaining 16 species of phocid seals (approximately half of the total number of pinniped species).

Stirling (1975) examined a range of ecological, behavioral, and physiological factors acting in various combinations, in an attempt to determine why some species became polygynous and others did not. Of particular interest were phocid seals that mated aquatically and gave birth to their pups on the ice. The key factors influencing the spatial distribution of females were accessibility to parturition habitat, type (terrestrial, landfast ice, pack ice) and stability of that habitat, and predation. More recently, reviews on the evolution of pinniped mating systems have tried to place pinnipeds within a broader mammalian context, to focus more attention on intersexual interactions, and to advocate a more detailed assessment of the environmental factors determining the temporal and spatial distribution of females (Boness 1991; Le Boeuf 1991). These studies provide the theoretical background for my research on the breeding behavior of the Atlantic walruses in the central Canadian High Arctic. Chapter 2 describes the breeding behavior of Atlantic walruses, compares my findings to what is known about Pacific walruses, *O.r. divergens*, discusses the ecological factors influencing the evolution of mating systems in walruses, and comments on how these findings contribute to our general knowledge of pinniped reproductive behavior.

1.2 STRUCTURE AND FUNCTION OF SONGS

Songs can be defined as loud, recognizable sequences of different sounds emitted during the breeding season, usually by males (Thorpe 1961; Nottebohm 1975). Song function has been defined as the way in which behavioral changes benefit the signaller by ultimately contributing to his survival and reproductive success (Smith 1977). In birds, songs can convey a wide range of information about the singer: species, individual identity, sex and age, singing location, that a male is ready to attack an intruder, or that he is ready to mate (Marler 1956). It is generally thought that song is used for territorial establishment and defense, mate attraction and maintenance of the pair bond, coordination of reproductive behavior between mates and within the population, signalling motivation, and species and individual recognition (Becker 1982; Beer 1970; Falls 1982; McDonald 1989). Each of these proposed functions has generated a vast and diverse body of literature. Three of the most pertinent areas relative to my research on the vocal behavior of Atlantic walruses concern the use of songs for territory establishment and defense, for mate attraction, and for individual recognition.

Trying to determine whether a male bird sings to establish or defend space, or to attract a mate, has been the focus of much research. Some biologists have emphasized the apparent dichotomy while others have suggested that the two functions are not mutually exclusive (Armstrong 1973; Catchpole 1982; Searcy and Andersson 1986; McDonald 1989). Understanding the duality of song function and its ultimate role in promoting reproductive success is currently an active topic of research and has shaped how we interpret other aspects of a bird's singing behavior. This is particularly true for studies that have addressed why some bird species have a large, complex repertoire while others sing only one simple song, and why some individuals within a breeding population have larger song repertoires than others (e.g., Howard 1974; Kroodsma 1976; Krebs 1977a and b; McGregor et al. 1981). The results of these studies indicate that both intersexual (female attraction), and intrasexual (successful territory establishment/defense) interactions appear to be important in the evolution of song repertoires. Attempts to understand the duality of song function have also focused attention on the fact that many bird species use different song types for intra- and intersexual behavioral interactions (e.g., Kroodsma et al. 1987; Mountjoy and Lemon 1991).

Most literature on the function and evolution of song pertains to birds, but many of the findings and theoretical concepts are relevant for other vertebrate species that have a song-like display. There are several species of marine mammals (other than walruses) that emit underwater songs during the breeding season. These include the humpback whale, *Megaptera novaeangliae*, bowhead whales, *Balaena mysticetus*, bearded seals, *Erignathus barbatus*, Weddell seals, *Leptonychotes weddelli*, and possibly leopard seals, *Hydrurga leptonyx* (Ray et al. 1969; Payne and McVay 1971; Ray and Watkins 1975; Stirling and Siniff 1979; Clark and Johnson 1981; Thomas and Kuechle 1982; Thomas et al. 1983; Stirling et al. 1987; Cleator and Stirling 1989). For most of these species, only the most basic details of song structure and organization are known. Chapter 3 documents variation in the structure and organization of songs emitted by mature male walruses singing in a variety of different environmental and social contexts and then discusses their behavioral significance and evolution.

1.3 INDIVIDUAL VARIABLITY IN VOCALIZATIONS

It is well established that bird individuals and species can be recognized by their songs (e.g., Nice 1943; Borror 1960). With the improvement of recording and analysis techniques it has become possible to quantitatively document individual variation and to demonstrate that birds can discriminate among the songs of other individuals in the absence of other identifying cues (Beers 1970; Falls 1982). In addition to birds, the use of individual differences in vocalizations to distinguish territorial neighbours from strangers has also been suggested in amphibians, fish, and in a variety of mammals (Myrberg and Riggio 1985; Conner 1985 a and b; Davis 1987). Other vertebrate species emit individually distinctive vocalizations, but it has not yet been demonstrated that they use these vocalizations to discriminate between neighbors and strangers, or other individuals. In birds, those species that show individual variation in their songs and can recognize neighbours and strangers, have also been shown to be able to recognize individuals (Falls 1982). Thus, it is likely that many more vertebrate species are capable of neighbor/stranger or individual recognition by sound.

The adaptive significance of individual recognition is broad in scope. Marler (1976) comments that strangeness is threatening and much of social behavior is devoted to increasing familiarity; recognition provides the opportunity for one individual to progressively learn about another over an extended period of time (e.g., the breeding season). The behavior of a familiar individual is more predictable and the social interactions of a group can be more finely tuned (Simpson 1973). Conflicts between individuals may be fundamentally different from those involving strangers, because deception is replaced by known asymmetries (Van Rhijn and Vodegel 1980).

In addition to these more general considerations individual recognition may allow an animal to conserve time and energy and to reduce the risk of injury by making informed decisions about when to fight (Falls 1982). Recognition may facilitate the reestablishment of territories or dominance status of an individual from one year to the next (e.g., Nolan 1978). The ability to recognize the vocalizations of a particular territory holder while remaining silent may be important for satellite males looking for an empty territory (Krebs 1976).

Several species of pinnipeds are known to have individually distinctive vocalizations, but as yet it has not been demonstrated that they recognize other individuals on the basis of these vocalizations (e.g., Stirling and Warneke 1971; Pierson 1978; Shipley et al. 1981; Trillmich and Majluf 1981; Cenami et al. 1992). The occurrence and function of individually distinctive whistles in small cetaceans have received considerable attention in the past (Caldwell and Caldwell 1965, 1971; Tarnski 1976; Tyack 1986). Recent studies have shown that free-ranging bottlenose dolphins, *Tursiops truncatus*, temporarily enclosed in a net corral, emitted indivually distinctive whistles (Sayigh et al. 1990). Long-term data on identified dolphins in those studies indicate whistles can remain stable for at least 12 years and appear to be important in maintaining the social structure of the community. There is considerably less known about individual variation in the vocal behavior of larger cetaceans (Watkins and Schevill 1977; Hafner et al. 1979; Dahlheim 1980; Weilgart and Whitehead 1988). Chapter 4 examines the structural variability of the surface coda (a distinctive underwater vocalization that is commonly heard and thought to be emitted by all mature males) and assesses whether individuals can be identified on the basis of this vocalization. The implications of individual recognition in relation to the breeding behavior of walruses are considered.

1.4 DISTRIBUTION AND ABUNDANCE

The Atlantic walrus is an abundant pinniped that is widely distributed in coastal waters of the eastern Canadian High Arctic, Hudson Bay, Baffin Bay and Davis Strait (Mansfield 1958; Loughrey 1959; Mansfield and St. Aubin 1991). During the openwater season walruses feed in shallow coastal areas and may haul out on land at traditionally-used sites. Most walruses overwinter and breed in remote inaccessible areas of drifting pack ice, such as in Baffin Bay or Davis Strait. However, some also overwinter and breed in polynyas - areas of open water surrounded by ice (Kiliaan and Stirling 1978; Stirling et al. 1983). The ice conditions and limitations on possible movements of walruses wintering in small polynyas may be different from those in the drifting pack ice. In a behavioral study, this is a particularly important consideration because variations in ecological factors that can affect the temporal and spatial dispersion of females are known to influence the evolution of social behavior (Chapter 2). Consequently, it is essential to have a sense of the size of the overwintering population and the constraints placed on their movements when interpreting the results of this study. Such information will also provide a baseline for comparison in future studies. In Chapter 5, I estimate the number of walruses overwintering in the Dundas Polynya and Penny Strait region during late winter, report on the distribution of walruses relative to sea-ice conditions, assess fidelity to overwintering sites, comment on the amount of time individual males spend in the polynya, and document the size and composition of walrus herds.

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2. THE BREEDING BEHAVIOR OF ATLANTIC WALRUSES IN THE CANADIAN HIGH ARCTIC

2.1 INTRODUCTION

All pinnipeds are polygynous in the sense that males will mate with more than one female whenever possible, and in species that have been well studied, there is considerable variance in male reproductive success (Boness 1991; Le Boeuf 1991). Research on the evolution of pinniped mating systems has established four primary ecological and phylogenetic determinants of pinniped polygyny: 1) aquatic adaptations (large body size, presence of subcutaneous fat) that allow exploitation of a marine food resource and promote the ability to fast, 2) the retention of terrestrial parturition which dictates various degrees of spatial aggregation at suitable breeding sites, 3) mammalian lactation which frees males from the constraints of parental care; and, 4) a postpartum oestrus and delayed implantation of the blastocyst which ensures at least moderate levels of oestrus synchronization (Bartholomew 1970; Stirling 1983; Boness 1991). Within this framework, current research has focused on determining how ecological and environmental factors influence the degree and form of polygyny via effects on female movements and dispersion and the degree of male competition (Stirling 1975, 1983; Heath and Francis 1983; Campagna and Le Boeuf 1988a, 1988b; Heath 1989).

The type of parturition habitat (land, pack ice or landfast ice) and whether mating occurs on land or in the water are two important factors shaping pinniped mating systems (Stirling 1975, 1983). All otariids (fur seals and sea lions) and three species of phocid seals (elephant seals, *Mirounga* spp., and the grey seal, *Halichoerus grypus*) typically mate and give birth to their pup on land. They are moderate to extremely polygynous and exhibit a resource or female defense mating system. All other phocid seals mate in the water and give birth to their pup either on land or on the sea ice. Those species which have been adequately studied appear to be slightly to moderately polygynous and are thought to have a serially monogamous or promiscuous form of mating system (Stirling 1975, 1983; Boness 1991; Le Boeuf 1991). Le Boeuf (1991) defines slight polygyny as the case when a male mates with 2 to 5 females, moderate polygyny when a male mates with 6 to 15 females, and extreme polygyny when a male mates with 16 to 100 or more females during a breeding season. The reduced level of polygyny in phocid seals is explained in part by the prevalence of aquatic mating and the difficulty of defending a resource or access to a female in a three-dimensional environment. Females are mobile, they have more control over the timing of mating and can be more assertive in mate choice. All these factors decrease the opportunity for males to monopolize large numbers of females (Stirling 1975, 1983). In addition, most phocid seals give birth to their pups on sparsely populated breeding beaches or on the sea ice, which is unstable and often highly variable in terms of suitability when compared to a parturition site on land. These factors limit the number and density of breeding females aggregating in an area and make it even more difficult for a male to defend a large number of mates. Details of the breeding behavior and the relationships between the different factors shaping the mating system of seals that mate in the water are not well understood. Seals that mate in the water make up approximately half of the 33 living species of pinnipeds and represent a serious gap in our understanding of breeding behavior and the evolution of mating systems.

Walruses provide a unique opportunity to study how sea-ice conditions, female aggregation and aquatic mating influence the degree of polygyny and the form of a mating system. There are two subspecies, the Atlantic walrus, *O.r. rosmarus*, and the Pacific walrus, *O.r. divergens*. Both subspecies are extremely gregarious and form herds that vary in size and composition depending upon the time of year and the population being studied (Mansfield 1958; Fay 1982). Breeding occurs in areas of unconsolidated, drifting pack ice or polynyas (an area of open water surrounded by stable landfast ice) during the winter from January to mid April. Females have a 15- to 16-month reproductive cycle (including a 4-5 month period of delayed implantation) and give birth to one calf every two or three years. Their reproductive cycle is one of the longest of any pinniped species and they are the only species that does not have a postpartum oestrus. In other pinnipeds mating occurs approximately two weeks after parturition; in walruses, oestrus females mate 3 to 4 months before females carrying full term fetuses give birth (Mansfield 1958; Fay 1982). How these unique life history-traits have shaped other aspects of walrus reproductive behavior are unknown.

Given that walruses mate in the water and give birth to their calf on the sea ice, one would predict them to be slightly polygynous and exhibit either a promiscuous or serially monogamous mating system. However, because females remain in herds during the breeding season there is potential for other forms of mating systems to evolve. Anecdotal observations on the Pacific walruses suggest that they are moderately polygynous and may have a mobile lek-like mating system (Fay 1982; Fay et al. 1984). During the breeding season female walruses and calves haul out on ice pans or rest in the water while one or more adult males station themselves in the water alongside a herd and perform complex underwater acoustic displays. The adult males repeatedly emit these vocalizations for as long as the females remain at rest. When more than one male attends a herd of females, they maintain a distance of about 7 to 10 m apart and vocalize from fixed stations. Each female appears to have the opportunity to choose which male she will approach, consort with and presumably mate with. Invasion of a male's display area by another results in visual agonistic displays and sometimes violent fighting. It has been assumed that the breeding behavior of Atlantic walruses is similar.

In this paper I describe the breeding behavior of Atlantic walruses, compare my findings to what is known about the Pacific walrus, comment on the ecological factors influencing the evolution of mating systems in walruses, and discuss how these findings contribute to our general knowledge of pinniped breeding behavior.

2.2 MATERIALS AND METHODS

2.2.1 Study area

Atlantic walruses overwinter and breed at a recurring polynya which forms just north of Cape Collins on Dundas Island (76° 09' N, 94° 52' W) in the central Canadian High Arctic (Kiliaan and Stirling 1978, Stirling et al. 1981; Figure 2-1). The size of the polynya varies seasonally and between years (Topham 1983). In February and March it is approximately 0.5 to 2.0 km long and 1.0 to 4.0 km wide. During April and May, the polynya increases to four or five times its initial size as ice breaks away from the edges. In extremely heavy ice years the polynya can be as small as 100 m long and 50 m wide, and on occasion, it will freeze over for several days at a time. The open-water area is surrounded by rough annual ice interspersed with smooth annual ice pans and some small multi-year ice floes (usually less than 100 m in diameter). Even in February and March when the ice cover appears to be solid, small holes, leads and sections of thin ice form within a 10-km square area around the polynya. During late winter the only other source of open water is a polynya located near Surprise Point on the northeast tip of Baillie-Hamilton Island, approximately 20 km south of the study site (Figure 2-1).

It is difficult to estimate the number of walruses overwintering in the Dundas Island polynya because few animals haul out during February and March and only a small proportion of the animals in the water are visible at any one time. From 25 to 65 walruses overwinter at the polynya except in heavy ice years when most, or all, walruses leave the area (Chapter 5). Bearded seals, *Erignathus barbatus*, and ringed seals, *Phoca hispida*, also overwinter in and near the Dundas Island polynya, but are not abundant and their presence does not affect walrus behavior observations or underwater vocal recordings. Polar bears, *Ursus maritimus*, also frequent the polynya and occasionally prey on walruses (Kiliaan and Stirling 1978; Stirling 1984; Calvert and Stirling 1990).

2.2.2 Data collection and interpretation

Observations on the breeding and vocal behavior of walruses at the Dundas Island polynya were made from 1981 through 1990 (Stirling et al. 1983, 1987, this study). Prior to 1987, field work was conducted from late March to May. In subsequent years observations were made from early February to May (Table 2-1). Observations were made from a hut located on a 80-m high cliff overlooking the polynya using 7 x 35 power binoculars and 15 to 60 power zoom spotting scopes (Figure 2-1). Underwater vocalizations and concurrent behavioral observations were recorded on a Uher 4200 Report Monitor tape recorder. An ITC 6050 hydrophone was suspended either through a hole in the ice or over the ice shelf along the edge of the polynya to a depth of 3 m.

When a herd of walruses swam into the polynya and could be viewed from the observation hut, five types of data were collected: 1) herd size, and sex and age composition, 2) the identity, location and movements of males associating with, or in the vicinity of, the herd; 3) the identity of as many other herd members as possible, 4) details of male-male or male-female interactions, particularly fights, threats, sexual displays, and courtship and copulatory behavior; and, 5) correlations between underwater vocalizations and breeding activities of the males. When a herd was composed of five or more active walruses it became impossible to monitor each individual. In these situations priority was placed on observing the behavior of the attending male and any walruses he interacted with. All data were collected opportunistically using the focal animal approach (Altman 1974). Data on herd attendance behavior of males was primarily based on visual observations. However, when a herd moved out of view, a compilation of acoustic data (confirmation of which male was singing), and visual observations (confirmation of which males were with the herd), provided additional information on how long a particular male attended a herd.

When a herd of walruses including at least one potentially breeding female and a mature, singing male (the attending male) frequented the polynya and observations or recordings were made, the data collection period was defined as a herd encounter. A group of three or more walruses was considered to be a herd. The activities of a herd were categorized as resting, milling, travelling, and possibly feeding. When resting, herd members maintained close contact and spent most of their time floating motionless at the surface. They usually formed a stationary, compact aggregation along the ice edge of the polynya. When milling, herd members maintained relatively close contact (within 10 m of each other) and spent most of their time diving asynchronously, playing, and swimming in a non-directional manner. They formed a slowly moving, loose (but still cohesive) aggregation that used areas within 100 m of the polynya's ice edge. Potentially feeding walruses did not maintain close contact (usually greater than 10 m apart); they dove relatively synchronously and spent most of their time underwater. They formed a mobile, dispersed group that frequented areas > 100 m off the polynya's ice edge. A travelling herd maintained relatively close contact, dove synchronously, and formed a relatively compact, elongated aggregation. The term "breeding activity" refers in a general way to courtship behavior, mounts and possible copulations.

Studying the breeding behavior and social organization of walruses was hampered in most years because of unsuitable ice cover, poor visibility conditions, location of the herds (too distant for observation), and prior to 1987, the lateness of the field season. The majority of the detailed observations on breeding activity discussed in this paper were collected in 1988 and 1989; one herd encounter was observed in 1988 and 18 in 1989 (Table 2-2). Approximately 85 hours of observations and concurrent underwater vocalization recordings were made during these 19 herd encounters. Between 1981 and 1987 an additional 21 herds were observed for a total of 100 hours. These latter observations were not as detailed as those made in 1988-89, but do serve as important supplementary and comparative data. Except where noted, these two data sets are analysed separately. In addition to observations of herds containing potentially breeding females and an attending male, another 700 hours of observations or concurrent recordings were made on 200 sightings of lone males singing in the polynya.

2.2.3 Walrus identification and estimation of ages

Most male walruses were identified using tusk characteristics and scars on the neck, shoulders, and back. Nine adult male walruses were immobilized and branded with two digit numbers on the hip and shoulder using copper cattle irons heated with a propane torch (Stirling and Sjare 1988). Few females were individually recognizable during the study because it was not possible to brand them and most did not have distinctive scars.

Determining the sex of young walruses, especially when they were in the water, was difficult. The morphological characteristics used included the shape of the tusks, the development of the neck and shoulder muscles, and the extent of blubber deposition in the upper neck region (Fay 1982). Even young males had more massive forequarters and stouter, more diverging tusks than females. When it was not possible to determine the sex with certainty, the walrus was described as a "presumed" male or female or as unknown. The age of males was estimated based on the relative size of the snout and tusks, the development of tubercles, and the muscular development of the upper neck and shoulders (Fay 1982). Walruses that were estimated to be 1 to 3 years of age and associated with a female were called calves. Male walruses with an estimated age of 4 to 8 years were called juveniles, those aged 8 to 15 years, young adults, and those older than 15 years, mature males (Fay 1982).

2.3 RESULTS

2.3.1 Social organization during the breeding season

In most years at least one or two herds of walruses containing potentially breeding females overwintered in the Dundas Island polynya. In 1988-89, the size of these herds varied from 4 to 15 walruses ($\bar{x}=9.1$, SD=3.1, n=19), and in 1981-87, from 3 to 43 ($\bar{x}=20.4$, SD=10.7, n=21). Females with calves formed the core of the herds, but juveniles of both sexes, presumed lone females, and young adult males were also present. In 1988 and 1989, 16 of 19 herds were composed of at least 40% females and calves

(Table 2-2). From February to early April the female component of the herd appeared to be relatively stable while the presence of juvenile and young adult males varied (Table 2-2). Female FRH and her calf were members of the same herd on a regular basis for at least a month; three other females (FSP1, FSP2, FAB) were also members for least a 2-week period (Table 2-2). From 1981-87, reliable composition data were collected on 7 of 21 occasions when a herd was in view. In all but one case females and calves composed at least 33% of the herd. Only limited data on the stability of the core herd are available for 1981-87. In 1981 a known female remained with one particular herd for at least three days. The herd in question was observed for nine days, during which time its size varied relatively little, suggesting that the female could have been a member for a longer period of time and that there may have been a stable core of females (Table 2-3). Herds observed from 1982-87 were either too distant or moved through the study area too quickly to allow identification of female walruses.

In 1988-89, all herds containing females were accompanied by a large mature male that sang incessantly in their presence. This attending male remained with the herd from several hours to six days at a time (Table 2-4). When walruses were milling or travelling (7/19) or when they were resting in the water (4/19), the male either mingled amongst them or swam along beside (usually within 10 to 20 m); if the herd hauled out on the ice (3/19) he stationed himself in the water 5 to 10 m away from the ice edge. When the herd was more dispersed (possibly feeding) the male often associated more closely with a particular female (perhaps one coming into oestrus) or a particular subgroup within the herd (5/19). In this situation he was often 20 to 60 m away from some herd members for much of the time. Attending males were the only male herd members that participated in any apparent breeding activities and they were also the only ones that sang continuously even though there were other young adult males present in the herd that were capable of doing so. Evidently, the presence of the attending male inhibited both sexual and singing behavior of the young adult male herd members. In 1981-87, observations on the presence and behavior of attending males were not as detailed or complete. However, in 18 of 21 herd observations there was enough evidence to confirm that one large, mature male was closely associated with the herd. Recordings made during some of these encounters indicated that there was only one main singer associated with each herd.

When an attending male and herd of walruses moved into the polynya there were usually several satellite males stationed 50 to 300 m away from them. All herd encounters in 1988-89 had at least one satellite male present for part of the time; the mean number present was 2.5 (SD=1.3, mode=2; range 1-5; n=19; Table 2-2). Even though observing satellite males was not a priority in 1981-87, at least one of these males was sighted in 11 of 21 herd encounters documented. Satellite males were either young adults or were mature males capable of challenging, and sometimes replacing, the current attending male (Table 2-2 and 2-3).

Satellite males exhibited three types of vocal behavior: they remained silent, they repeatedly emitted short fragments of their song in sporadic outbursts, or they continuously sang their full song. Because of this variability, the type of background vocalizations recorded during each of the 1988-89 herd encounters differed. In 5 of 19 encounters satellite males were predominantly silent but did emit sporadic outbursts of song fragments; in 9 of 19 encounters they alternated between singing full songs for a variable length of time and being silent; and, in the remaining encounters they repeatedly emitted outbursts of song fragments, sang full songs, and occasionally remained silent. Outbursts of song fragments lasted for 0.17 to 10 min (n=33) and sometimes involved more than one singer. When satellite males were singing full songs it was usually impossible to monitor how long each sang because of the extensive overlap between individuals. However, two general patterns emerged: they either sang as long as the attending male did, or they sang for 0.15 to 1.5 hr when the herd moved into or out of the observation area.

When the satellite males were not singing it was difficult to keep track of their location. They often remained in the area for as long as the herd remained, while at other times they left after one or two sightings. Sometimes there was no sign of any, and then suddenly, several would appear. Data on the locations of known satellite males were collected during herd encounters in 1989. In 9 of 12 cases, satellite males moved into or out of the area once the herd established itself. In 7/9 of those cases the number of satellite males was highest when the herd first arrived in the observation area, and then dropped the longer the herd remained. A sudden, loud, outburst of song fragments and excessive grunting by females, calves and juvenile walruses appeared to attract satellite males regardless of how long the herd had been in the area (n=4).

When herds containing breeding females were not present in the polynya or surrounding area, mature males either sang alone or near a herd of juveniles and young adult males hauled out on the ice. When singing alone, males usually stationed themselves along the ice edge of the polynya or in a haul-out hole near the polynya. They sang at a particular location anywhere from 0.5 to 24 hr (Chapter 3) and then moved to another area, continued to sing, or became silent. Although displaying males roved around the polynya and surrounding area and did not defend specific territories, they did space themselves. It was common to hear up to five males singing concurrently; however, in most cases only one or two could be seen from the observation hut.

2.3.2 Behavior of males

Interactions between mature males

Only a few males were able to control the access of other males to a herd for any length of time. In 1989 during a 5-week period in February and March, 14 vocal males were identified, of which four established themselves as attending males. In 1988, 11 vocal males were identified, of which two established themselves as attending males. All six were large individuals that sang extensively throughout the breeding season and were thought to be at least 15 years of age (Table 2-5). Descriptions of the males attending herds in 1981-87 were less detailed, but it was evident that they were also mature, large, and well scarred. Although there were several walruses in the polynya capable of holding the attending male position at one time during the breeding season, one individual spent significantly more time with the herd. In 1989, walrus 8903 held the attending male position on 12 of 18 days when females were in the area. The other three males (8907, 8910, and BR02) combined, attended a herd for the remainder of the time (Table 2-6). During the herd encounter observed in 1988, the attending male was displaced during a fight by a large, mature satellite male (described as a successful herd take-over interaction). It was not possible to tell which of the two males spent more time with a herd during the breeding season. In 1981, two males were identified and observed associating with a herd over a 9-day period (sufficient information on their activities was collected on seven of those days). One male assumed the attending male role on six of the seven days.

Herds containing females were attended by a series of males that replaced one another every 1 to 5 days; one particular male dominated the rotation. Table 2-4 presents the herd attendance profile for the four males that were observed with a herd in 1989. These profiles are based on a compilation of data collected when the herd and attending male were in view, and on acoustic and other observational data collected when the herd was distant. Between 13 February and 15 March, male 8903 was displaced from an attending male position 4 or 5 times, males 8907 and 8910 were each displaced twice, and BR02 once (Tables 2-2 and 2-4). The discrepancy for male 8903 arises because he attended a herd on 8 March and from 11-15 March. Bad weather prevented observations and recordings from being made on 9 and 10 March so it is not known if he remained with the herd for the entire 7 days. If 8903 did remain for the whole time, then the mean number of consecutive days he spent with a herd during February and March was 3.5 (SD=3.0, n=4); if he did not, his attendance was 3.0 (SD=2.0, n=5). The other three males were not with a herd for such long periods: 8907 attended a herd for approximately 1 day on two different occasions; 8910 attended a herd for 2 days on one occasion and for approximately 2 hrs on another; and BR02 attended a herd for 1 hr only (Tables 2-2 and 2-6). Attendance profiles for mature males recorded in 1981-1988 could not be constructed because there were no data on known individuals or too few observations of herds. However, in 1981 at least one attending male was displaced and then regained his position, and in 1988, male BR04 was displaced during a fight (it was not known if he became an attending male again some time later).

After an attending male was displaced, it usually was not possible to document the interactions leading up to his reestablishment as an attending male. Most mature males have scars and superficial bleeding wounds on their neck and shoulders, but surprisingly few fights (n=4) and only one herd take-over interaction were observed. In late April 1988, a silent, mature satellite male (BR01) closely approached a female herd member. This action incited an intense fight between him and the attending male (BR04). One male reared out of the water to about mid-chest height and attempted to drive his tusks into the neck region of the other male. After striking one another two or three times the pair came together and rolled around at or near the surface of the water. It was difficult to see details of the encounter, but it appeared as though one walrus was trying to remain on top of the other (perhaps trying to hold the other individual underwater to disrupt breathing). The fight lasted about 2.5 min and when it was over the former attending male (BR04) became silent and left the area by himself while the satellite male (BR01) took over his position and sang for at least the rest of the afternoon. Both males had fresh wounds prior to the fight indicating they had been involved recently in aggressive interactions (not necessarily with each other).

Where an attending male goes and what he does after he has been displaced is not known. In 6 of 18 herd encounters observed in 1989, male 8903 was not the attending male. During three of those encounters he was seen in the vicinity of the herd behaving as a predominantly silent, satellite male (Table 2-2). His location was not known during the other three herd encounters. Fewer data on the activities of the other three attending males are available. On five of the days when 8907 was not attending a herd, he was a satellite male; his location during the other 11 herd encounters was unknown. Male 8910 was a satellite during six herd encounters and not seen in nine others. Male BR02 was a satellite in only one of the herd encounters and seen once as a satellite male (Table 2-2). During the last half of April mature males are known to haul out between periods of attending a herd and between long bouts of displaying (Chapters 3 and 5). It is possible that on some of the occasions when 8907 and 8910 were not attending a herd or behaving as satellite males, they were either silently resting in the water or they were hauled out somewhere in the polynya area. They may have also been singing in different areas of the polynya quite distant from the attending male and herd under observation.

Although a dominance hierarchy likely existed among the mature males, ranking individuals was difficult because too few direct interactions between identified walruses were observed. However, if the most dominant individuals are the ones that have the greatest access to females and have the best opportunities to mate successfully, then in 1989, walrus 8903 was the dominant male since he spent the most time associating with females. Males 8907 and 8910 ranked second and third, and BR02 fourth (Table 2-6). Similar rankings were obtained when the number of days spent in the study area, and when the number of hours of recorded singing, were compared between the males (Table 2-6). It was not possible to infer the social status of mature males that were never observed attending a herd by using number of days spent in the study area or number of hours of recorded singing as indices. Unlike the attending males, these males did not appear to center their singing activity in the area of the polynya that could be viewed from the observation hut. Some males were only seen and recorded briefly once or twice (<2.5 hrs). Data on the social status of males observed and recorded in 1981-88 are not available because there were too few observations of herds and most attending males could not be identified. However, it is worth noting that the two attending males (BR04 and BR01) identified in 1988 were also the most vocal males throughout the breeding season.

The response of lone, mature, singing males to the approach of an attending male and herd or another singing male showed that males listened to the songs of others and that subtle interactions were mediated through singing behavior. On 5 occasions in 1989, an attending male and herd moved from another area of the polynya to within 300 to 800 m of a lone, mature, singing male. In all cases the lone singer either temporarily disrupted his song or became silent and then moved away from the area. When 8903 was the attending male he displaced 8907 and 8906 on two occasion each; when 8910 was the attending male he displaced 8907 once. The activities of displaced males were usually unknown; however, on one of the occasions when 8903 displaced 8907, 8907 stayed in the general area and behaved as a silent satellite male for 0.75 hrs and then was not seen again. When females were not present in the polynya, lone mature males slowly moved about the polynya while singing. On 20 occasions since 1981, singing males have been displaced by another singing individual approaching from several hundred meters away. Although there were too few of these interactions involving known individuals to establish a hierarchy, some males sang longer from one location, or maintained their singing locations, even when background vocalizations were moderately loud (indicating another male was approaching). In 14 of 20 cases where a male was displaced, the younger or noticeably smaller male left the area. These observations suggest that the spacing and movements of singing males are influenced by dominance-related interactions between the males. The movement of singing males around the polynya area was typical throughout the breeding season in all years of the study. Thus, subtle displacement interactions likely occurred more frequently than was documented.

Interactions involving young adult males

In the presence of an attending male and females, young adult male walruses spent time as silent herd members, or as satellite males, or they alternated between the two positions. During the herd encounters observed in 1989, six young adults were identified on at least 3 different days (Table 2-2). Males 8908 (n=14) and 8911 (n=5) were always seen as silent herd members. Males 8904 (n=9) and 8913 (n=3) were predominantly satellite males that emitted sporadic outbursts of songs and also sang continuously for various lengths of time throughout the breeding season. In 2 of 9 herd encounters (21/02/89 and 26/02/89) 8904 played with juvenile herd members briefly (<0.5 hr) before leaving the herd and becoming a satellite male. During a herd encounter on 8 March male 8913 was first identified as a satellite male, after which he approached the herd and surfaced several times near 8903 (the attending male at the time), then after 0.15 hr, he left the herd and behaved as a vocal satellite male again. Male 8912 (n=4) spent time as both a herd member and a satellite male on 26 February and 1 March, was seen briefly as a satellite male on 8 March, and then was a silent herd member on 12 March. Male BR11 (n=3) was a silent herd member on 5 and 6 March and then was seen as both a herd member and a satellite male on 8 March. There were no obvious male-male interactions that appeared to influence whether a particular young male spent more time as a herd member or a satellite male.

There are no comparable data on the behavior of identified young adult males during herd encounters in 1981-1987, but the presence of young adult was confirmed in at least 8 of 21 herds observed. During the herd encounter observed in 1988, male BR11 was sighted in the area; his behavior was similar to that in 1989. He was first identified as a silent satellite male, then he approached the herd and engaged in play activity with the juvenile herd members. After approximately 1 hr, he left the herd and was not seen again.

As long as young male herd members remained silent and did not initiate any courtship activities, or approach mature females too closely, the attending male appeared to ignore them. In 1988-89 there were no aggressive interactions involving physical contact between the attending male and young adult male herd members. However, attending males chased young adult males when they approached a female too closely or vocalized. In 1988-89 the mean hourly rate of chase interactions during a herd encounter was 0.69 (SD=0.51; range=0.31-1.96; n=11; Table 2-7). The younger male ended up being displaced 20 to 80 m, but within minutes he would rejoin the core herd. Often a full chase never developed, instead, the attending male simply oriented his body towards the younger male, or he oriented his body and swam slowly in the direction of the younger male who then immediately moved away from the female (n=13 observations; Table 2-7). This interaction was described as a body threat display. Attending males continued to sing even when they chased or threatened a younger male.

Even though the attending male usually ignored young adult male herd members, some of the younger males closely monitored his movements and avoided him. In 1989, some young adult males surfaced more often on the side of the herd that was farthest away from the attending male and appeared to be using other herd members as a shield. At other times, they surfaced and dove at the same spot the attending male had just left; the young male appeared to be following along behind the attending male but was always one or two surface locations away. These interactions were subtle and difficult to quantify consistently; however, they were observed in 12 of 18 herd encounters in 1989. When the attending male dove to emit the underwater portion of his song, some young adult males moved closer to a female herd member and, on rare occasions, actually initiated courtship behavior. When the attending male surfaced the young male quickly moved several meters away from the female or dived underwater. In 1988-89 the mean hourly rate of this type of evasive interaction during a herd encounter was 1.28 (SD=1.49; range=0.32-5.70; n=12; Table 2-7).

Not all young males in a herd participated in these types of interactions to the same degree. In 1989, male 8908 was displaced in 19 of 25 chases, involved in 38 of 42 evasive behavior interactions, the recipient of all the body threat displays (n=13), and was the only young adult male herd member that tried to initiate courtship behavior with a female when the attending male was underwater. Male 8908 was a predominantly silent herd member when 8903, 8907 and 8910 were attending males; all three appeared to monitor his activities closely. The only other younger male that received a noticeable amount of attention from an attending male was 8912. All other younger males spent most of their time playing with juvenile herd members and generally milling about with the herd.

In almost all cases, the young adult satellite males observed in 1988-89 did not physically interact with the female herd members or attending male. However, during one herd encounter a silent young satellite (male 8913 on 8 March) approached the herd. He ignored the female members and proceeded to swim back and forth in front of the attending male at a distance of about 2 to 5 m. He swam towards the attending male several times head-on and broadside, while the attending male appeared to ignore him and continued to sing uninterrupted. After approximately 0.15 hr the younger male left the herd and stationed himself about 100 m away and sang sporadically for at least 1.5 hr.

One aggressive, physical interaction between two satellite males was observed in early March, 1989 (the identity of the individuals was not confirmed but at least one individual was a young adult male). The two walruses were approximately 100 m apart when they started swimming quickly towards each other. They met, fought for 0.5 min, and then both submerged and were not seen again. Prior to the interaction, both males were singing sporadically but afterwards only one continued.

Interactions involving sexually immature walruses

The attending males observed in 1988-89 were tolerant of calves and small juveniles (usually the sex was unknown); they allowed young walruses to crowd around them, roll on top of them, and even attempt the occasional mount ($n=2$), without showing signs of aggression. These types of interactions were most common when the herd was relatively large ($>$ 5 walruses), compact and actively milling along the edge of the polynya. Judging from the structure and activity level of herds observed in 1981-87 and the fact that the attending males sometimes surfaced in the middle of the herds, it is likely they also tolerated young walruses. Juvenile male herd members sometimes stationed themselves 5 to 10 m from the attending male and proceeded to surface and dive, and occasionally breath, in synchrony with him. The young walrus usually remained silent, but on occasion, did emit a few knocking sounds. The attending male showed no signs of aggression towards the juvenile. This behavior was described as shadowing and it occurred in 7 of 19 herd encounters in 1988-89. It was difficult to identify the young walruses participating in this behavior but at least three different individuals were involved during a one month period. Although observing the detailed behavior of juvenile walruses was not a priority in 1981-87, there was evidence of shadowing in 3 of 21 herd encounters. Juveniles also shadowed mature males when they were singing alone in the absence of females. In 1981-87, 3 of 137 males sighted singing were shadowed by a juvenile or young adult walrus. Another 24 singing males had at least one silent, usually younger, male associating with him (50 to 200 m away). In most cases it was not known if these males dove and breathed synchronously with the singer.

2.3.3 Interactions between males and females

Courtship behavior and copulation

During courtship the male and female synchronized their dives and engaged in close-contact parallel swimming (usually within 0.5 m of each other). In addition, the male often placed his foreflipper on the female's mid-back while swimming or, if the female was stationary, when he first approached her (i.e., flipper touching). When a male attempted a mount he rolled slightly on his side and placed his foreflippers around the female's mid-section and forcefully pulled her close to the ventral surface of his body. Sometimes the pair remained in this position for several seconds and then broke apart. At other times the male maintained his grip and rolled on top of the female. A less common mounting technique involved the male submerging underwater and quickly swimming towards a female lying at the surface. When the male was directly underneath her he rolled onto his back and clasped the female around her mid-section with his foreflippers and forcefully attempted to pull her towards him. At this point the pair either broke apart or the male attempted to roll on top of the female.

Probable copulation was observed only once during this study. On 12 March 1989, male 8903 mounted a female for between 0.5 and 2.5 min, 8 to 10 times during a 2-hour period. At least three of these mounts may have resulted in successful copulation; the male's hips were curled around the female's hindquarters and pelvic thrusts were seen. During copulation the female was submerged and out of view, while the male remained at the surface with his shoulders, upper foreflipper region, and back visible. His position in the water was similar to the one males assume while singing except that his back was slightly more arched, he floated higher in the water, and he appeared to be grasping something underwater with his foreflippers (when a male sings at the surface, only the arched dome of the mid-back region is visible). Throughout the duration of the interaction the male continued to sing, but he spent more time at the surface compared to when he was singing alone.

Courtship behavior or mounts were observed in 8 of 19 herd encounters observed in 1988-89 and in 3 of 21 encounters in 1981-87. Nineteen mounts and 8 incidents of flipper touching were observed during 19 herd encounters in 1988-89. When the 12 March (when probable copulations were observed) herd encounter was excluded from analysis, the mean number of courtship interactions and mounts observed per hour was 0.67 (SD=0.56, n=7; Table 2-7). In 3 of 8 herd encounters in 1988-89 when the attending male was sexually active, some of the presumed male juvenile herd members and calves also appeared to become sexually excited and mounted other juveniles or calves (n=9). Juvenile walruses behaved similarly during the three herd encounters that had a sexually active attending male in 1981-87.

Based on observations of herds frequenting the polynya between 13 February and 3 April 1989 (n=18), breeding activity was highest from 22 February to 1 March, and from 12 to 15 March (Table 2-7). The occurrence of herds in the area of the observation hut and singing by attending males declined noticeably after 20 March, even though one herd encounter was observed on 3 April. In 1988, walruses centered much of their activity in an area 5 to 10 km W and NW of the observation area so it was not possible to collect data on the breeding activity except on 25 April. The two attending males were dominant singers throughout the breeding season and were probably the dominant males in the polynya. This suggests that in some years breeding may occur in late April. Evidence of breeding activity was also observed on 5 and 7 April in 1981 and on 15 April in 1983, but the age and social status of the attending males was unknown.

Female choice, herd defense and solicitous behavior

By the time a herd was sighted in the polynya an attending male was already present. Thus, the importance of female choice, if any, in determining which male initially monopolized the herd is unknown. Usually it was difficult to tell whether the females or the attending male controlled the movements of the herd or if all individuals simply moved together. On three occasions in 1989 when an attending male abruptly left the herd and swam towards a singing satellite male, the herd changed their swimming direction and followed him, suggesting that he had some influence on herd movement. In two herd encounters observed in 1989 (19 February, and 3 April) the females remained with the attending male for only 0.45 to 1.0 hrs and then left the area and were not seen again. In both cases the males did not attempt to follow them or impede their movements suggesting that, in at least some situations, females have considerable freedom. The attending males at the time were 8910 and BR02, the third and fourth most dominant attending males in 1989. Limited observations suggested that females were attracted to singing males, and that only vocal males could control access to a herd. During the herd encounters on 6 and 7 March when 8910 was the attending male and 8903 was a silent satellite male stationed about 50 m from the herd, no females attempted to associate with 8903. Given that he had been the attending male for a good portion of the previous two weeks (Table 2-2) it was likely that the females knew he was still in the area.

Although the number of females and calves varied during some of the herd encounters observed in 1988-89, no females left the herd to associate with any of the satellites or vice versa. Attending males did not appear to herd or chase the females together; the cohesive nature of herd seemed to stem more from the gregariousness of the females. There are no data on the movements and behavior of female herd members relative to potential herding behavior by males in 1981-87, but their gregariousness was evident in those years as well. On two occasions in 1989 when 8907 and 8910 were attending males (23 February and 7 March) both exhibited behaviors that could be interpreted as a type of herd defense. At the time there were two or more satellite males singing loudly nearby and both attending males appeared to become excited and behaved more aggressively. They rarely sang from the same location for more than two surface/dive cycles, they swam faster and more erratically (abrupt changes of direction while at the surface), covered greater distances while swimming underwater, and sang from positions located farther away from the herd (20 to 60 m). These activities contrasted noticeably with 8903's typical attendance behavior. When 8903 and a herd were milling along the edge of the polynya he usually sang from a single location within 20 m of the core herd of females and calves. When he moved his swimming behavior was slow and controlled. The highly charged activity levels of 8907 and 8910 parallelled a noticeable change in the behavior of the herd members in which they bunched together, with the females and calves taking up positions closer to the center of the herd. It was not clear whether they were responding primarily to the change in behavior of the attending male or to the vocalizations of the satellite males, or both. Females and calves also bunched together if the attending male chased a young male herd member.

Unless an attending male and female were involved in courtship behavior it was difficult to pinpoint any specific interactions between them. Females appeared to ignore the young adult males in the herd even though they regularly associated closely with them. If a young male (8908) initiated courtship behavior, there was no obvious indication that the female attempted to incite an interaction between him and the attending male. Solicitous female behavior was not observed commonly, but it did occur. In 1989 a young presumed female (no calf) swam repeatedly under the attending male and rolled onto her back so that the ventral surfaces of both animals were almost in contact. She held this position for several seconds and then abruptly surfaced in front of the male and proceeded to swim back and forth in front of him. The attending male appeared to ignore her and continued to sing.

2.4 DISCUSSION

2.4.1 Comments on the mating system of Atlantic walruses

Following the definition of Emlen and Oring (1977), observations on Atlantic walruses breeding at the Dundas Island polynya suggest their mating system is more similar to female-defense polygyny than to a lek. Large mature males defend and appear to compete for exclusive access to herds containing potentially reproductive females. In the presence of the attending male, young adult male herd members remain silent and curtail their sexual activities; satellite males generally do not approach within 50 m of the attending male. The occurrence of satellite males in the vicinity of a herd is variable. They often sing atypical songs in sporadic outbursts regardless of their age, and do not behave as potential attending males attempting to attract females. In addition, many satellite males appear to be too young to secure an attending male position.

Although these observations suggest a female-defense mating system, additional data on dispersion of displaying males and on female choice must also be considered. Four criteria are commonly used to distinguish leks: 1) males contribute nothing to the next generation except gametes, 2) most mating occurs in an arena that represents a small fraction of the available habitat used by females, 3) display sites or territories of males within the arena contain no significant resources required by females except the males themselves, and 4) females have an opportunity to select mates when they come into the area (Bradbury 1981). The first criterion is generally true for Atlantic walruses, but the remaining three are problematic.

Defining a display arena is difficult because, when there are no females in view, the males roam around the entire polynya and surrounding area while singing. Much of the time the display arena virtually fills the polynya and there is no separation between the arena and the habitat normally used by the females during the winter. Furthermore, the Dundas Island polynya is one of only a few places where walruses can overwinter in the entire Penny Strait region. Walruses must have reliable access to open water to breathe during the winter; therefore, the whole area might be considered as critical winter habitat for walruses of both sexes and all age classes. For criteria two and three to be applicable to the walruses at Dundas Island, either the definition of what constitutes a critical resource must be relaxed or the definition of the walruses' display arena must be more stringent; neither is entirely acceptable on the basis of the available data. Based on the limited amount of data available, it appears that females do not assess and choose a mate in a manner similar to Pacific walruses or other lekking species of birds and mammals. They do not leave the herd and attending male to approach or consort with any of the satellite males even if one of those males happened to be a former attending male. Nor do they consort with lone males singing within 1-5 km of a herd. It seems likely that a female will mate with the male that is attending the herd when she becomes receptive. These observations do not preclude the occurrence of more subtle forms of female choice; this possibility is discussed further in the section on the importance of female aggregation during the breeding season.

Several problems hampered efforts to detect whether or not female choice occurred. Although no female herd members were seen consorting with males other than the attending male, some females left or joined a focal herd. The activities and whereabouts of the females before and after joining the herd were unknown. It is possible that they were in the process of changing herds, they had been hauled out, or they were about to haul out. Data collection was further hampered because only one herd was close enough for detailed observation at any one time. Consequently, females either had to associate with the attending male or one of the satellites. Given this limited social context and what is known about the behavior of satellite males, observing any evidence of choice was unlikely. To determine if female choice occurs it will be necessary to observe the herd-attendance patterns of females when two or more herds are present and there is the option of switching herds and attending males. It is also possible that some important male-female interactions occurred near the beginning of the breeding season in late January or early February and were missed due to the late start of the field seasons.

In summary, because these data do not adequately support three of the four criterion used to distinguish leks, and one male clearly monopolizes a herd for extended periods of time, the mating system of walruses at the Dundas Island polynya is best described as female-defense polygyny rather than a lek-like mating system.

2.4.2 Comments on the social organization of Atlantic walruses

Herd attendance by mature males

For mammalian species that have a female-defense mating system, breeding males must either reside with a particular group for extended periods of time or move between groups, examining each for receptive females. A number of factors will affect the male's choice, but the likely criterion for determining which strategy is followed will be the expected number of successful matings achieved during the breeding season (Whitehead 1990). Using a theoretical model Whitehead (1990) concluded that males should remain resident with groups of females if the travel time between encountering groups of females is greater than the oestrus period of a female, and otherwise the male should rove. If female group size varies, or males can anticipate female receptivity, then males should remain with groups where there is a high immediate probability of successful matings, and leave those where it is low. This is particularly true if there is a well established dominance hierarchy among the males and the cost of regaining control of a herd is minimal in terms of energy expenditure and risk of injury.

The herd-attendance profiles of males are generally consistent with the predictions. The most dominant male (8903) spent most of his time attending a herd, but did leave it periodically to rest, sing alone, and possibly attend another herd in another area of the polynya. When males 8907 and 8910 (the second- and third-ranked males) were not attending males, they behaved as satellite males in 30 to 40% of the herd encounters. During the remainder of the encounters they sang alone some distance away, rested, or may have attended another herd. When 8903 was not the attending male, his position was taken by one of these males almost immediately. Males 8907 and 8910 must have been carefully monitoring his activities (possibly by listening to his singing behavior) to be able to either displace or replace him so quickly. It was not evident whether attending males were able to assess the reproductive status of the females in the herd; naso-anal investigative behavior was not observed, but other more subtle cues may have been used. Short-term fatigue and a longer-term requirement to conserve enough energy to compete successfully for the entire breeding season were probably critical factors in determining how long 8903 attended a herd (Bartholomew 1970; Le Boeuf 1974; Deutsch et al. 1990). Male 8903 was replaced as attending male four or five times between mid February and mid March. However, the lack of fresh wounds on his back and neck indicated that reestablishing himself as the attending male probably did not involve excessive fighting.

Behavior of satellite males and young adult male herd members

While there is often one reproductive strategy that yields the highest reproductive success for a given sex, some less successful individuals may use alternative strategies to maximize their immediate or future chances of mating (Boness 1991). Secondary mating strategies have been reported in otariid species and, as with other animals, individuals exhibiting them are smaller and usually younger (Peterson 1968; Marlow 1975; Gisiner 1985; Campagna et al. 1988). Young adult male walruses and less successful mature male walruses engaged in three behavioral activities that could be considered alternative reproductive strategies. Some males spent most of their time either as a silent herd member or as a vocal satellite male, while others alternated between the two positions. Although it was not possible to age the males accurately, it was apparent that in most cases the smallest and youngest males behaved as silent herd members and the more mature males as satellites. However, there were some exceptions. As previously mentioned, males 8907 and 8910 (known attending males) were regularly seen as satellite males, but they also spent much of their time in other activities. Male 8908 was a young adult male that always behaved as a silent herd member. Considering his size and abundance of scars, it was surprising that he never vocalized as a satellite male.

Given that singing appears to be an essential component of being an attending male, and that a male's social status may be conveyed by his vocal behavior, there is likely a reproductive cost associated with being a silent herd member or a satellite male that sings sporadically. However, silent herd members are able to associate closely with females in the herd. Since some females remain with the same herd for 2 or 3 weeks at a time, young adult males would have the opportunity to become familiar with the behavior of several individual females on a seasonal basis. In addition, there appears to be some limited opportunities for certain silent herd members to steal copulations from the attending male. The manner in which some young adult males shadow the attending male while he sings, and sometimes appear to monitor his movements, suggests that they are learning from or mimicking him. Such learning experiences could enhance a young adult male's chances of becoming dominant. Satellite males do not have the opportunity to closely associate with the females, but the most dominant of them may be in a position to challenge the attending male or to take-over his position when he departs. This is probably the most significant advantage of being a satellite male.

There were no obvious interactions between individuals that appeared to dictate whether a male behaved as a silent herd member, a vocal satellite male, or sang alone some distance away from the herd. A male's behavior may be determined by which other males are in the area and how they are singing at the time. This hypothesis assumes males can recognize each other and that they can assess each others competitiveness or fighting ability. On the basis of observations presented in Chapters 3 and 4, this seems likely. For example, if 8903 were the attending male and had been with the herd for only one day and was not fatigued, then the chances of a herd take-over by another male may be low. In such a situation, it would be a good strategy for males 8907 and 8910 to roam around the polynya looking for another herd rather than sing sporadically as satellite males. In contrast, if 8903 had been attending a herd for longer, the chances of a successful challenge might be higher. In this circumstance, males 8907 and 8910 should choose to remain in the area as satellite males because the chance that one of them could become the new attending male would be greater. This hypothesis is adapted from data on the roaring behavior of red deer. Clutton-Brock and Albon (1979) showed that the roaring rate was an honest indicator of fighting ability. As some males became exhausted during the course of the breeding season their roaring rates declined; males that were in better condition appeared to recognize the change and took advantage of the fatigued males' reduced fighting ability.

2.4.3 Comparisons between the mating systems of Atlantic and Pacific walruses

The mating system of the Pacific walrus differs in several respects from that of the Atlantic walrus breeding at the Dundas Island polynya. In Pacific walruses, a higher number of displaying males station themselves within 10 to 20 m of the females and no one individual appears to monopolize access to the herd. Males actively defend small display territories near the herd, and the frequency of fighting seems to be higher than seen in Atlantic walruses. Thus, female Pacific walruses may have the opportunity to assess and then choose one of the displaying males as her mate. On two separate occasions Fay et al. (1984) observed a young presumed female approach and consort with two displaying males and then submerge underwater with one of them. It was not possible to determine if mating occurred. Those observations suggest that the mating system of Pacific walruses is more lek-like than that of Atlantic walruses.

However, several important points must be emphasized with regard to available data on the breeding behavior of Pacific walruses. First, over a 4-year period Fay et al. (1984) were able to observe ten occasions when one or more males were displaying in the immediate vicinity of a herd. In six cases only one male was present, in another, three males were spaced about 40 to 80 m apart, and in the remaining three, six to eight males were spaced approximately 10 m apart. Second, the evidence for female choice is limited. And finally, underwater vocalizations were not monitored for most of these observations so it was not known if all males were singing full songs or just shadowing a more dominant individual.

In six of the ten observations reported by Fay et al. (1984), the breeding behavior of Pacific male walruses was similar to that of Atlantic walruses. The remaining four observations suggest that something different was occurring, but to date, data are insufficient to evaluate whether or not these differences are adequate to justify describing the mating system of Pacific walruses as being lek-like. More quantitative information on how frequently multi-male aggregations occur, the prevalence of female choice, and whether or not all males sing, is required before this question can be addressed adequately. Nevertheless, with the information available from the two species, it is possible to consider how social and environmental factors might be responsible for the differences observed in the mating systems of the two subspecies.

The density of walruses in an area and the type of sea- ice habitat are likely to be significant factors. About 50 walruses are thought to overwinter and breed in the vicinity of the Dundas Island polynya. Except for another polynya of similar size about 20 km to the south of Dundas Island, the area is surrounded by thick, stable first-year ice. From

January through March, when walruses breed, temperatures are the coldest of the year and sea ice attains its maximum thickness and coverage. Such ice conditions appear to limit the movements of walruses throughout the surrounding area and result in a relatively sedentary population concentrated near the polynya during the breeding season (Chapter 5). Under this circumstance displaying males have the opportunity to interact with all potential competitors and establish a dominance hierarchy. Because females are gregarious, the most dominant males are able to monopolize access to the few herds in the polynya and control the behavior of their competitors.

The Pacific walruses observed in the breeding season by Fay et al. (1984) were in drifting pack ice where the distribution of open water was constantly changing. The density of walruses in an area comparable in size to the Dundas Island polynya could easily be ten times as high (estimate based on Fay et al. 1984). The dynamic nature of the sea ice, and the higher numbers of relatively mobile males, may make it difficult for stable dominance relationships based on individual recognition to be established. Under these conditions it would be very difficult and energetically expensive for one male to maintain exclusive access to a herd of females (Emlen and Oring 1977; Byers and Kitchen 1988). As a result, the most dominant males crowd close to the females and aggressively defend small territories. With so many large herds of relatively mobile females in an area males may opt to display near several herds for brief periods, rather than continuously follow and defend one herd.

The role of stable vs. dynamic sea-ice conditions in shaping the mating system of walruses is plausible given what is known about the evolution of mating systems in other pinniped species (Stirling 1975; Boness 1991). The relationship between sea-ice habitat and the number, density, and mobility of walruses is probably mediated via foraging behavior. Although mature, breeding males feed very little during the winter breeding season, females must have access to food (Fay 1982). The extent and stability of ice cover determine the accessibility of the walruses' benthic food resource. In unconsolidated drifting pack ice habitat, walruses are constantly being moved over new feeding areas, and the everchanging configuration of leads and open water provide virtually unlimited access to their food resource. In a polynya bounded by landfast ice, potential feeding areas are restricted, and occur in approximately the same area each year.

Thus, the number of walruses each polynya area could sustain through the winter is likely to be limited.

Studies on a wide range of vertebrates have shown that increased density of resources or mates, and increased male-male competition, in a resource-defense system can lead to reduced territory size or even territory breakdown (Wilson 1975; Bradbury 1981; Davies and Houston 1981; Wittenberger 1981; Stamps 1983; Byers and Kitchen 1988). For species that exhibit female-defense polygyny, an increase in male-male competition causes the male to lose control over part of his herd. At some point, the cost of defending the remaining females outweighs the benefits of monopolizing access to them, and alternative strategies are adopted (Emlen and Oring 1977; Bradbury 1981; Boness 1991). Beehler and Foster (1988) suggest that intense male-male competition can play an important role in the development and maintenance of a lek. The premise of their "hotshot" model is that, in species exhibiting female-defense polygyny, it is common for some males to be more successful at acquiring mates because of certain behavioral (e.g., singing endurance) or morphological attributes (e.g., body or tusk size). The less successful males cluster around these more dominant individuals, and as a result, obtain more mating than they would if they displayed alone. Data on the breeding behavior of walruses suggest that this model may provide a useful framework for developing hypotheses about the selective pressures that could influence a shift towards a lek-like mating system. To confirm the effects of high densities of displaying males and females and sea-ice habitat on mating system form it will be necessary to study the breeding behavior of walruses of both subspecies in populations that vary in size, density and the type of breeding habitat used, especially pack ice vs. polynya.

2.4.4 Plasticity in the reproductive strategies of walruses

Some level of plasticity in the reproductive strategy of a species is thought to be adaptive because it allows accommodation to changing environmental or social conditions (Trivers and Willard, 1973; Wilson 1975; Emlen and Oring 1977; Boness 1991). A number of vertebrate species show inter-population variations in mating system (Lott 1984). However, until recently, studies of pinnipeds have not adequately addressed this issue. Observations on Weddell seals, *Leptonychotes weddelli* (Smith and Burton 1970; Kaufman et al. 1975; Siniff 1979), grey seals (Hewer 1960; Curry-Lindahl 1970;

Anderson et al. 1975; Boness and James 1979), and harbour seals, *Phoca vitulina* (Venables and Venables 1955, 1957, 1959; Bishop 1968; Burns 1972) suggest that the level of polygyny and perhaps the form of mating system vary between populations depending on the type of parturition habitat available (land, landfast ice or pack- ice). Detailed comparative studies have not been completed for any of these species. Recent studies on California sea lions, *Zalophus californianus* (Heath 1989) and Southern sea lions (Campagna and Le Boeuf 1988a and 1988b) have shown that beach topography and temperature (as it relates to the thermoregulatory demands of females) may lead to inter-population variation in the reproductive behavior and form of mating system. As more information becomes available on the breeding behavior of Pacific walruses and other populations of Atlantic walruses, it is likely that their reproductive strategies will prove variable in relation to habitat.

Studies on the reproductive strategies and mating systems of several species of ungulates have shown intra-population variations (e.g., Rubenstein 1986; Gosling 1986; Byers and Kitchen 1988; Clutton-Brock et al. 1988; Thirgood 1990). Similar studies are not available for pinnipeds. However, it is noteworthy that of the six mammalian species known to have a lek mating system, five are ungulates. In each species, lek breeding occurs only in some populations, and within any single population, only a portion of mature males hold territories on leks while others maintain larger resource territories in adjacent areas or defend females (Gosling 1986; Clutton-Brock et al. 1988). Given the possibility that some Pacific walruses may have a lek-like mating system, these observations may be relevant for interpreting walrus breeding behavior in the future.

2.4.5 Female gregariousness and the evolution of mating systems in walruses

Besides the walrus, the only other moderately polygynous species of ice-breeding seal with a female-defense mating system is the Weddell seal (Kaufman et al. 1975; Siniff 1979). Female Weddell seals are not normally gregarious, especially in comparison to species such as walruses or elephant seals. However, they clump together more closely during the breeding season because the number of self-maintained breathing holes is limited compared to later when the ice begins to break up (Stirling 1969; Kaufman et al. 1975). In this circumstance males successfully defend underwater territories that encompass the breathing holes and mate with the females using them. Therefore, even though Weddell seals mate aquatically and breed in a spacious and seasonally variable habitat, the necessity for females to aggregate around breathing holes has enabled a moderately polygynous mating system to evolve. A somewhat similar situation occurs in walruses. Individuals of both sexes are gregarious during both the breeding and non-breeding season (see Fay 1982 for review; Taggart 1987). It is generally thought that predator avoidance, increased foraging efficiency, and phylogenetic factors have influenced the evolution of gregariousness in female walruses during the breeding season (Stirling 1975, 1983; Fay 1982; Taggart 1987). Female gregariousness has facilitated the evolution of a moderately polygynous mating system in walruses under ecological circumstances that have precluded such systems from developing in other ice-breeding pinnipeds.

Female gregariousness in itself may be a subtle, indirect way of expressing choice (Beehler and Foster 1988). Observations on Atlantic walruses suggest that a female will mate with whichever male is attending the herd when she comes into oestrus. An effective way for females to maximize the chance of mating with successful males is to be in a herd with several other potentially oestrus females. Because of the dominance relationships among the males a large herd containing several oestrous females is likely to attract and incite competition between the most reproductively successful males. Thus, by remaining in a herd with other oestrus females, a female ensures that she has the opportunity to breed with a dominant male. The herd attendance profile of a dominant male shows that he attempts to maximize his time with a herd throughout the breeding season; this behavior further improves the chances of a female herd member mating with a dominant male.

Boness (1991) noted that in otariid species where females are mobile there is a tendency for a lek-like mating system to evolve (Campagna and Le Boeuf 1988a and 1988b; Heath 1989). In phocid seals that have aquatic copulations and may be widely dispersed as well, there is a tendency for female-defense polygyny to evolve (Boness and James 1979; Siniff et al. 1979; Stirling 1983; Boness et al. 1988). Boness suggests that this difference may occur because female density among otariid species is higher than among phocids, making a female-defense system too costly for male otariids. Observations on the breeding behavior of walruses provide some support for this hypothesis. Atlantic walruses breeding in low numbers in a relatively stable sea-ice environment exhibit a female-defense system while some Pacific walruses breeding at much higher densities may have a lek-like mating system. The mean herd size of Atlantic walruses at Dundas Island was 20 (n=21) in 1981-1987, and 9 (n=19) in 1988-1989. In Pacific walruses, the mean size of herds with only one displaying male was 25 (SD=16.6, n=5), and with more than one male 175 (SD=116.3, n=4; Fay et al. 1984).

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Table 2-1. Summary of field-season dates, ice conditions and behavioral observations at the Dundas Island polynya.

First and last date of field season (d/m/y)	Ice Conditions[**]	Relative Abundance of Walruses in the Immediate Study Area[+]	Opportunity to Observe Breeding Behavior[++]
02-23/04/1981	suitable	high	excellent
04-21/04/1982	polynya too small	few or none	nil
08-26/04/1983	suitable	moderate	good
05-25/04/1984	suitable	moderate	fair
12/03-10/04/1985	polynya too large	few or none	nil
06/04-01/05/1986	suitable	moderate	fair
23/02-22/05/1987	polynya too large	few	poor
13/02-12/05/1988	suitable	moderate	good
09/02-29/04/1989	polynya large	high	excellent
12/02-03/03/1990	polynya too small	few or none	nil

[**] During extreme ice years when the polynya is small walruses leave the area; when the polynya is large the walruses disperse over a large area and are difficult to observe.

[+] Even when ice conditions are suitable it is often not possible to observe walruses because they are using areas that are several kilometers from the main polynya.

[++] Opportunities to observe courtship and mating activites are influenced by the ice conditions and the number of walruses in the main polynya near the observation hut.

Table 2-2. Summary of herd sizes and composition for 1988-1989.

Date (d/m)	Herd size	Percent group composition (n)	Identity of attending male	Identity of female(s)	Identity of male herd member(s)	Identity of satellite male(s)
14/02	10	20 (2) F/C 60 (6) JUV 10 (1) YAM	8903	FRH	8908	2 UNKNOWN
19/02	5	80 (4) F/C	B02	2 UNKNOWN	NONE	8903
20/02	9	22 (2) F/C 67 (6) JUV	8903	FRH	NONE	8904,8906
21/02	11	55 (6) F/C 27 (3) JUV 9 (1) YAM	8903	FSP1 FSP2 1 UNKNOWN	8908,8904(b)	8904,8907
22/02	12	50 (6) F/C 25 (3) JUV 17 (2) YAM	8903	FRH FAB 1 UNKNOWN	8908,8911	8904,8910 2 UNKNOWN
23/02	4	50 (2) F/C 25 (1) YAM	8907	1 UNKNOWN	8908*	8904 1 UNKNOWN
26/02	15	53 (8) F/C 27 (4) JUV 13 (2) YAM	8907	FSP1 FRH FAB 1 UNKNOWN	8908,8911 8904(b) 8912(b)	8910,8912,8904 2 UNKNOWN
01/03	13	62 (8) F/C 15 (2) JUV 15 (2) YAM	8903	FRH FSP1 FSP2 1 UNKNOWN	8908,8911 8912(b)	8912,8907,8910
03/03	12	67 (8) F/C 8 (1) JUV 17 (2) YAM	8903	4 UNKNOWN	8908,8911 8906(b)	8907,8904 8906,8910
05/03	8	63 (5) F/C 13 (1) JUV 13 (1) YAM	8903	FRH 2 UNKNOWN	BR11(b)	1 UNKNOWN
06/03	10	40 (4) F/C 20 (2) JUV 30 (3) YAM	8910	FRH FAB	BR11(b) 8908 1 UNKNOWN	8904,8903 1 UNKNOWN
07/03	6	67 (4) F/C 17 (1) YAM	8910	FRH FSP1	8908	8904,8907,8903
08/03	10	60 (6) F/C 30 (3) YAM	8903	FRH FSP1 1 UNKNOWN	8908,8913(b) 8911,BR11(b)	8913,BR02,8910 BR11(b),8912(b)
12/03	12	50 (6) F/C 25 (3) JUV 17 (2) YAM	8903	FRH 1 UNKNOWN	8908,8912	8907
13/03	6	67 (4) F/C 17 (1) YAM	8903	2 UNKNOWN	8908	8904

Date (d/m)	Herd size	Percent group composition (n)	Identity of attending male	Identity of female(s)	Identity of male herd member(s)	Identity of satellite male(s)
14/03	11	55 (6) F/C 18 (2) JUV 18 (2) YAM	8903	3 UNKNOWN	8908 1 UNKNOWN	2 UNKNOWN
15/03	6	67 (4) F/C 17 (1) YAM	8903	FRH 1 UNKNOWN	8908	8910 1 UNKNOWN
03/04	5	20 (1) F 20 (1) YAM 40 (2) JUV	8910	1 UNKNOWN	1 UNKNOWN	2 UNKNOWN
25/04 1988	6	67 (4) F/C 16 (1) JUV	BR04	2 UNKNOWN		BR01**; BR11 1 UNKNOWN

F/C female with calf; JUV juvenile; YAM young adult male

(b) seen briefly
* sometimes behaved as a satellite
**BR01 challenged BR04 and took over the herd.

Identity names assigned to individual females:
FRH; FAB; FSP1; FSP2

Table 2-3. Summary of herd sizes and composition for 1981-1987.

Date (y/m:d)	Hours of Observation	Herd Size	Comments on Herd Composition
1981/04:			
3	4.5	30-35	no comments
4	5.5	30-40	no comments
5	8.5	40-45	67% females/calves
6	14.5	40	no comments
7	12.0	35	no comments
8	9.5	20	no comments
9	8.0	20	no comments
10	7.0	30	40% females/calves; 50% juveniles; 10% adults
1983/04:			
4	2.5	20-25	no comments
10	2.5	8	no comments
15	0.8	13	no comments
15	2.0	15-20	no comments; different herd
1984\04:			
7	1.0	20	at least 20% females/calves
16	1.5	4	50% females/calves; 25% young adult males
1985\04:			
9	1.5	15	at least 40% females/calves
1986\04:			
11	1.35	20-25	no comments
12	1.0	15	at least 40% females/calves
15	1.0	7-10	no comments
1987\03:			
3	1.0	10	no comment
14	1.5	10	40% females/calves; 20% juveniles or females
15	12.0	30	at least 33% females/calves; 40% juvenile or young adult males

Table 2-4. Herd-attendance profiles for 8905, 8910, 8901 and BR02 in 1989.

Date (m:d)	Comments On Herd Attendance
02:13	8903 lone singer
14	8903 attends herd
15	8903 lone singer
16	8903 lone singer
17	8904 and 8905 lone singers; whereabouts of 8903 unknown
18	no observations; 8903 may be singing in distance
19	BR02 attends a small herd for 1.0 hour
20	8903 attends herd
21	8903 attends herd
22	8903 attends herd
23	8907 attends herd
24	no herd in area; 8907 sings along
25	no herd in area; 8907 and 8903 lone singers
26	8907 attends herd
27	no herd in area; 8903 singing in distance
28	bad weather, no observations
03: 1	8903 attends herd
2	8903 attends herd
3	8903 attends herd
4	8903 attends herd
5	8903 attends herd
6	8910 attends herd
7	8910 attends herd
8	8903 attends herd
9	bad weather; no observations
10	bad weather; no observations
11	8903 attends herd
12	8903 attends herd
13	8903 attends herd
14	8903 attends herd
15	8903 attends herd
	no herds seen until April 3
04: 3	8910 attends herd

Table 2-5. Summary of sightings and physical characteristics of identified males in 1989.

Walrus identification	Earliest and latest dates seen (d/m)	Number of days observed**	Relative age	BSI***	Tusk length (cm)	Tubercle development+	Neck scar index+	Back scar index+
8805	27/03 04/04	6	M	3	35	5	5	3
8901	11/02	1	M	3			4	4
8903	13/02 15/04	25	M	3	40	5	5	3
8904	17/02 07/04	11	YAM	1	25-30	2	3	2
8905	17/02 04/04	3	YAM	1	25-30	2	2	2
8906	20/02 27/02	5	M	3	45	5	4	4
8907	21/02 25/03	19	M	3	40	5	4	4
8908	12/02 20/04	24	YAM	2	30-35	2	3	2
8910	22/02 04/04	10	M	3	40-45	5	5	5
8913	08/03	1	YAM	2	30-35	3	3	3
BR02	19/02 08/03	2	M	2		3	3	3
BR11	05/03 10/03	4	YAM	2		3	3	2

** The number of days the male was observed in the polynya.

*** Body size index: 1 = small; 2 = medium; 3 = large.

+ Tubercle and scarring index: 1 = very light; 2 = light; 3 = moderate; 4 = moderate to heavy; 5 = heavy.

M mature male

YAM young adult male

Table 2-6. Details on the behavior of attending males in 1989.

Walrus Identification	Days in Study Area	Percentage of time spent as attending male (N)	Hours spent vocalizing	Total days spent with herd
8903	61	67 (12/18)	100	14.0
8907	41	17 (3/18)	56	2.0
8910	32	11 (2/18)	16	2.5
BR02	17	5 (1/18)	6	0.5

Table 2-7. Occurrence of breeding activities and aggressive interactions exhibited by attending males in 1988-1989. The number of observations in each herd encounters and the rate of occurrence of different behavioral acts are shown.

Date (y/m:d) of herd encounter	Hours of observation	Breeding activities/hr** (n)	Chases/hr (n)	Evasive tactics/hr (n)	Body threat displays/hr (n)
1989/02:					
14	2.50			0.80 (2)	
19	1.00				
20	2.67		0.37 (1)	0.37 (1)	
21	7.17		0.70 (5)	1.53 (11)	0.12 (1)
22	2.95	0.68 (2)	0.34 (1)	1.34 (1)	
23	3.00		0.33 (1)		0.33 (1)
26	1.58	1.9 (3)	0.63 (1)	5.70 (9)	1.90 (3)
1989/03:					
1	3.83	0.26 (1)			
3	1.87			0.53 (1)	
5	3.00				
6	1.70				
7	3.12		1.28 (4)		1.60 (5)
8	2.20		0.45 (1)	0.91 (2)	
12	2.61	6.13 (16)	1.96 (5)	0.38 (1)	
13	2.07		0.48 (1)		0.48 (1)
14	2.65	0.38 (1)		0.38 (1)	
14	1.57			1.91 (3)	
15	3.20	0.64 (1)	0.31 (1)	1.56 ((5)	0.31 (1)
1989/04: 3	2.38	0.42 (1)			
1988/04: 25	5.20	0.39 (2)	0.78 (4)	0.98 (5)	0.91 (1)

** Breeding activities included: touching flippers, mounts and possible copulations.

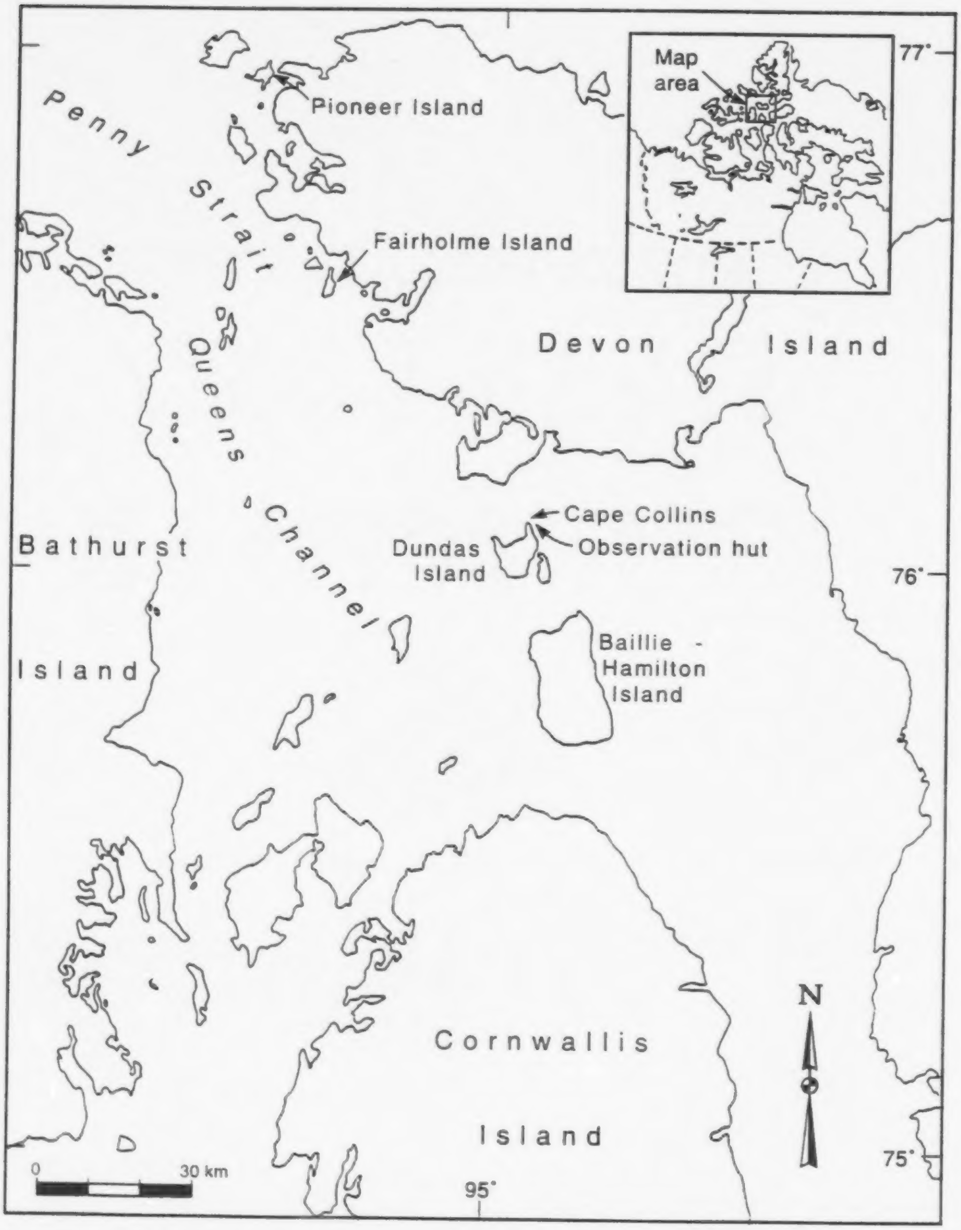
Map area
77°
Pioneer Island
Penny Strait
Queens Channel
Fairholme Island
Devon Island
Bathurst Island
Cape Collins
Dundas Island
Observation hut
76°
Baillie - Hamilton Island
N
Cornwallis Island
0
30 km
95°
75°

Figure 2 - 1. Map of the study area.

3. VARIABILITY IN THE SONGS OF MATURE MALE ATLANTIC WALRUSES IN THE CANADIAN ARCTIC.

3.1 INTRODUCTION

Most gregarious species of pinnipeds are highly vocal during the breeding season and Atlantic walruses are no exception. The underwater song of a male walrus consists of several long, patterned, sequences of pulses that are punctuated with ringing bell sounds. Most of the song is emitted while the male is completely submerged; however, a portion is given while he floats at the surface with his head submerged between breaths (Schevill et al. 1966; Ray and Watkins 1975; Fay 1982; Stirling et al. 1983, 1987). Some of the pulses sound like knuckles being rapped firmly and slowly against a wood surface and are best described as knocks while others sound more like taps (Stirling et al. 1983). Knocks have a frequency range of approximately 200 to 8000 Hz with most of the sound energy distributed below 2000 Hz, and a repetition rate of 1 - 3/s. Taps have a frequency range of approximately 200 to 4000 Hz and a repetition rate of approximately 15/s (Stirling et al. 1983). The pattern of knocks and taps in each long sequence, and the order in which the sequences are emitted, are consistent within and among individuals, and between years (Stirling et al. 1983, 1987).

Two main song types have been described, the coda vocalization cycle and the diving vocalization cycle (Stirling et al. 1983, 1987). These types differ in the pattern of knocks and taps composing each of the long sequences, and by the presence or absence of specific vocalizations called surface codas, underwater bell-knock codas, and diving vocalizations (Schevill et al. 1966; Ray and Watkins 1975; Stirling et al. 1983, 1987). These vocalizations are brief, distinctive series of intense knocks that either begin or end a long knocking and tapping sequence. When a walrus sings a coda vocalization cycle many of the sequences emitted at the surface end with a surface coda while certain underwater sequences end with a bell-knock coda. When a walrus sings a diving vocalization cycle no surface codas or bell-knock codas are given during the song, but a distinctive series of loud knocks is given just after he dives; this diving vocalization leads into the first long underwater sequence (Stirling et al. 1987).

Knowledge of the singing behavior of walruses is based on only a few individuals that were recorded once or twice. The objectives of this paper are to quantify the structure and consistency of coda and diving vocalization songs from a larger sample of males recorded under a diverse range of environmental and social contexts. Emphasis is placed on assessing the relationships of recording date and the presence of females and other singing males on the structure and duration of songs. The evolution and behavioral significance of songs is discussed.

3.2 MATERIALS AND METHODS

3.2.1 Study area and recording techniques

Twenty-five to 65 Atlantic walruses overwinter and breed at a recurring polynya that forms north of Cape Collins on Dundas Island (76° 09' N, 94° 52' W) in the central Canadian High Arctic (Kiliaan and Stirling 1978; Stirling et al. 1981; Chapter 5; Figure 3-1). Ice conditions in the area have been described in Chapter 2. Observations and recordings were obtained from a hut located on a 80-m high cliff over-looking the polynya. All underwater recordings were made using a Uher 4200 Report Monitor tape recorder and an International Transducer Corporation 6050C hydrophone. The effective frequency response of the recording system was either 25 - 12,000 Hz at a tape speed of 4.7cm/s or 20 - 16,000 Hz at a tape speed of 9.5 cm/s. For long recording sessions or those made for investigating daily trends, a tape speed of 4.7 cm/s was used; if better quality was required the speed was increased to 9.5 cm/s. The hydrophone was either submerged through a hole in the ice or lowered to a depth of 3 m from an ice shelf along the southern edge of the polynya near the base of the cliff. Vocalizations were analysed on a Multigon Uniscan II and Kay Elemetric 7800 Sonagraph with a 150 Hz analysing filter bandwidth.

3.2.2 Data collection and observational techniques

The underwater breeding vocalizations of walruses at the Dundas Island polynya have been recorded from 1981 through 1990 (Stirling et al. 1983, 1987; this study). Prior to 1987, field seasons ran from late March or early April into May. In 1987, field work started in early February; exact field dates for all years are given in Table 2-1. The analyses presented here are based on recordings of 23 identifiable males made between 1983 and 1989 (Table 3-1). Songs from all mature males recorded in 1988 and 1989 were included in the data base. Males recorded before 1988 were selected for analysis if they sang for a long period of time or were recorded on at least three occasions; however, their songs were not included in any between-year comparisons. Two males were recorded in more than one year: male 8301 in 1983, 1984 and 1987; and male 8805 in 1988 and 1989.

The polynya was monitored both visually and acoustically during the day and acoustically during the night when a focal walrus was being followed; recordings were made whenever a singing male moved into the study area. Priority was given to recording from identifiable males if there was a choice. When possible each focal walrus was recorded continuously for 2.5 hours (which, in most cases, would allow for the documentation of at least 20 songs). If the singing male remained in the study area for longer, additional 1.5-hour recording sessions were taped two or three hours apart or whenever there was a change in his social behavior. When a singing male remained in the area for more than 24 hrs and sufficient recordings had been made, his songs were monitored and transcribed by hand (monitoring session). Focal walrus recordings and monitor notes were supplemented with a series of briefer recordings to document vocal activity on a seasonal basis; they were also used to follow the singing behavior of a focal male over a long period. From 1987 to 1989 these sessions were 30 min long and were recorded every three hours on a 24-hour basis for approximately 15 days at the beginning, middle and end of the field season. Before 1987, they were 20 min long and were recorded every two hours. The recording period was extended to 30 min to ensure that at least 4 complete songs would be recorded from singing males.

Most male walruses were identified using drawings of tusk characteristics and scar patterns on the neck, shoulders and back. In addition to these natural marks, nine males were immobilized and branded with two-digit, 12.5 cm high, numbers on their hip and shoulder (Stirling and Sjare 1988). Age and sex of walruses were determined using the relative size of the snout and tusks, muscular development of the upper neck and shoulders, and presence and development of tubercles (Fay 1982).

A total of 3034 vocalization cycles (songs), were analysed in detail. All good recordings were used, except for extensive samples. In those cases, approximately 15 songs were selected from each of the beginning, middle, and end of a singing bout. If a male was recorded several times during the season, songs from the beginning, middle and end of singing bouts taped early in the season, mid season and late in the season were analyzed for comparison. Thus, for males that sang extensively, it was possible to determine if songs varied with recording date and the length of a singing bout.

The social contexts in which males were recorded often varied considerably, both within a recording session and between days. The most common contexts were: singing alone with no other males visible within 100 m; singing in the presence of a silent male that remained within 50 m; singing when vocal satellite males were near; and singing in the presence of females and calves. During most recordings, it was possible to hear one or more additional males singing at some distance from the focal walrus. Background vocalizations were classified as "faint" if only a small portion of the loudest part of the song could be heard, "moderately loud" if portions of an entire song sequence could be recognized and easily followed, or "loud" if the background vocalizations were almost indistinguishable from those of the focal walrus. By sub-sampling data for males recorded in different contexts, it was possible to evaluate how songs varied contextually.

3.2.3 Measurement and statistical analysis of walrus songs

Songs can be defined as loud, recognizable sequences of different sounds emitted during the breeding, usually by males (Thorpe 1961; Nottebohm 1975). Since the vocalizations of mature male walruses fit these criteria of a song, this term is used instead of "vocalization cycle" hereafter (e.g., coda vocalization cycle = coda song). One full song includes both an underwater and surface portion. The surface portion of the song was considered to be from the time the male's head broke the water for the first breath to the time he dived. The underwater portion was from the time he dived to the time he surfaced again for his next breath. The duration of one full song was considered to be the interval of time between surfacings. Under good observation conditions, it was possible to see the male rise to the surface to and note when his head broke the water for the first breath. Under poor observation conditions, or if the male moved behind an ice floe out of view, his surface and dive times were estimated on the basis of his vocalizations. The interval between the end of the last underwater knocking sequence and when a male surfaced for his first breath was consistent for an individual. Similarly, the interval between the end of the last knocking sequence emitted at the surface and the onset of a dive was also consistent. On those bases, I estimated times that could not be recorded directly. Whenever possible, surfacing and dive times, plus behavioral observations, were recorded on the second track of the tape. During a monitoring session, surfacing and dive times were documented along with the transcribed song.

Coda songs were distinguished from diving vocalization songs (DV songs) based on differences in the pattern of knocks and taps composing each long sequence, and by the presence or absence of surface codas, underwater bell-knock codas, and diving vocalizations (Stirling et al. 1987). Different variations of each song type were described on the basis of the number and order in which the long, underwater sequences were emitted. In almost all cases the terminology used to describe the variations of each song type or any distinctive vocalizations follows Stirling et al. (1987). The most notable exception is that the double-knock bell (dkb) described in 1987 is now referred to as a double-knock bell-knock (dk-bk) since there are clearly three pulses with the tonal component associated with the terminal pulse. Bell-like tonal sounds are rarely emitted without at least one preceding pulse.

Mann-Whitney U tests (MWU), Kruskal-Wallis (KW) analyses of variance, and Tukey multiple comparisons (SAS 1988; Zar 1974) were used to test whether songs varied with: recording date; presence of nearby females or silent males; duration of singing bout; and the intensity of background vocalizations. The song variables used for the comparisons included: total duration; duration of the surface and underwater portion of the song; proportion of time spent at the surface; and number of breaths taken. For analyses on groups of walruses (e.g., mature males vs. attending males) the song variable means for the individual walruses in the group were averaged to give an unweighed estimate. G-tests were used to determine if the frequency of occurrence of different song types and variations varied with any of the above factors. However, this test was not used to access the relationship of between-year differences or the importance of relative age and social status to proportion of song types emitted. To avoid pooling songs emitted by males in a year group or age group, KW or MW-U tests were used to make comparisons between similar song types and variations. An alpha level of 0.05 was used for all tests.

3.3 RESULTS

3.3.1 Variations in the structure and organization of walrus songs

Mature male walruses overwintering and breeding at the Dundas Island polynya sing four qualitatively different song types: coda songs; diving vocalization songs (DV songs); intermediate songs; and aberrant songs. There are four easily recognized coda-song variations as well: short, typical, long, and erratic. The structure and organization of the first three coda-song variations are consistent within and among all males frequenting the polynya. Erratic coda songs may be individually specific, but their exact structure and organization are not shared by all males. Each coda song variation is distinguished on the basis of the underwater portion of the song since it is the longest and most complex part of the vocal display. Figure 3-2 illustrates the surface and underwater portions of a typical coda song. The underwater portion is composed of four long sequences of consistently patterned knocks and taps punctuated with ringing bell sounds. Each sequence can be recognised easily by the intense and distinctively patterned series of knocks and associated tonal sounds that terminate it; sequence I ends with a bell-knock coda (bkc), sequence II with a double-knock-bell-knock (dk-bk), sequence III with another variation of bell-knock coda (bkc), and sequence IV ends with bell-knocks (bks) and a distinctive double-knock (dk). The number of knocks and taps composing each of the long sequences ranges from approximately 20 to 600 and there is considerable variation within and between individuals.

In the short coda song, sequence III is consistently omitted. In the long coda song, sequences II and III are repeated so that the order of sequences becomes: I, II, III, II, III, IV (Figure 3-2). The structure of an erratic coda song is easily recognized as a coda song, but may have sequences that are emitted in a slightly different order, long periods of silence throughout the song, highly variable number of breaths at the surface, and irregular changes in the rhythm or duration of the song.

Few males in this study emitted the DV song; however, a sufficient number of recordings were made to confirm that the overall song structure and organization was similar to that described by Stirling et al. (1987). The underwater portion of the song is composed of six sequences which usually terminate with a bk or a knock-strum (k-strum; Stirling et al. 1983, 1987; Figure 3-2). The pattern of knocking and tapping series in each of the long sequences is different from that of the coda song and there are no bell-knock codas (bkc) emitted. It was not possible to confirm with certainty how many consistent and shared variations of this song there are. However, in addition to the typical DV song, males also sang a short variation where sequences III, IV and V were consistently omitted. Unless stated otherwise, these two variations were combined for analyses.

When males sing underwater they sometimes switch from a coda song to a DV song (or vice versa), and on rare occasions, they will do a double switch - coda to DV and then back to coda (or vice versa). Stirling et al. (1987) described these vocalizations as intermediate songs (Figure 3-2). Their structure and organization are often consistent within an individual, but not shared by all males in the polynya. Switches occur most often during the first half of the underwater portion and usually in the middle of a long knocking or tapping series. Unless stated otherwise all intermediate songs were combined for analysis.

In addition to coda, DV, and intermediate songs, males also emit aberrant songs that are characterized by long periods of silence, lack of pattern in the knocking and tapping series composing a sequence, lack of consistency in the order of sequences, and the occurrence of uncharacteristic sounds (e.g., loud grunting or groaning). These songs cannot be recognized as any of the previously described songs types, they usually are not consistent within an individual, and they are not shared by most males in the polynya. The strum-vocalization song described by Stirling et al. (1987) was not recorded in this study.

Although the different song types and variations are best described on the basis of the underwater portion of the song, the surface portions of both the coda and DV songs also show considerable variation. In the coda song the surface portion is lengthened or shortened by repeating or omitting one or more of the k 4k or k 4k--ts--coda sequences (Figure 3-2; typical coda song - labelled 1 and 2 respectively). The order in which these two sequences are emitted and the length of the tapping sequence (ts) leading into the surface coda varies. Similar variations occur in the DV song; the duration of the surface portion depends on how many k k sequences are emitted and how long the k--ts--2k sequence is (Figure 3-2; DV song - sequences labelled 1 and 2 respectively).

Switches and double switches between coda and DV songs can occur during the surface portion of a song. When the male sings a coda song the switch usually occurs during the tapping series leading up to the surface coda and in the DV song it usually occurs during the tapping series leading up to the 2k (Figure 3-2).

Occasionally the singing behavior of a male is inconsistent during the surface portion of the song. He may take noticeably more breaths with either no vocalizations, or long pauses between sequences; make radical changes in the length or repetition rate of the ts leading up to the surface coda or 2k; or emit uncharacteristic sounds. Surface portions that were sufficiently inconsistent to confound the recognition of the song were described as aberrant. If there was a switch in the surface portion of a song it usually carried over into the underwater portion, and the full song was classified as intermediate. Because a song with an aberrant surface portion usually had an erratic or aberrant underwater portion as well, the full song was classified as an erratic coda song or aberrant song.

3.3.2 Frequency of occurrence of song types and variations

Most males emitted a large proportion of the entire repertoire of songs; however, only 7 of 23 males emitted DV songs, and of those, five sang them on a regular basis (> 12.5% of the time; Figure 3-3). Intermediate songs were also not as common; only 8 of 23 males sang them. Figures 3-4a and 3-4b summarize the percent occurrence of each song type or variation on an individual basis. Of the 20 males that emitted coda-song variations, 18 sang them 60 - 100% of the time. For most males, typical and short coda songs were the most commonly emitted; three males (8904, 8907, 8502) had high proportions of erratic coda songs in their repertoire. Three other males, 8807, BR04, and BR01, sang exclusively DV songs, and males 8607 and 8801 sang DV songs 27% and 13% of the time respectively (Figure 3-4a and 3-4b). When all song types and variations were categorized as either stereotyped or non-stereotyped, 19 of 23 males sang stereotyped songs at least 75% of the time (Figure 3-4c and 3-4d). Stereotyped songs included DV songs and short, typical, and long coda songs. Non-stereotyped songs included erratic coda songs, intermediate songs, and aberrant songs.

There were shifts in the occurrence of certain song types and variations between years (Table 3-2). A greater proportion of typical coda songs (MWU test, $p=0.02$, $n=10, 11$) and fewer DV songs (MWU test, $p=0.02$, $n=10, 11$) were emitted in 1989 than in 1988. Only two males, 8305 and 8805, were recorded in more than one year.

Although sample sizes were small for male 8305 (some song variations had to be combined for analysis), there were no between-year differences in the proportion of song variations emitted (G-test, p=0.41, df=4, n=13, 27, 38; Table 3-3a). Male 8805, however, sang more typical coda songs, and fewer DV and intermediate songs in 1989 as compared to 1988 (G-test, p=0.001, df=4, n=185, 240; Table 3-3a).

3.3.3 Variability in song duration

When songs of each male were combined, the mean duration ranged from 3.94 - 9.34 min (grand mean 6.22, SD=1.45, n=23; Figure 3-5). Tables 3-4 and 3-5 summarize data on total song durations for the song types and variations emitted by each walrus. When the total durations of the different songs sung by a each male were compared to the male's typical coda song some basic trends were apparent. Short coda songs were 1.43 min (SD=0.45, n=19 males) shorter than typical songs, and long coda songs were 1.40 min (SD=0.62, n=10 males) longer than the typical song. In 6 of 7 of the cases when a male emitted both intermediate and typical coda songs, the intermediate songs were 0.76 min (SD=0.15, n=6) longer. Diving vocalization songs were 0.57 - 1.93 min longer than the typical coda songs in the 3 males that sang them regularly. In 7 of 10 cases where males emitted aberrant songs, they were between 1.09 and 7.00 min ($\bar{x}$=2.99, SD=2.01) longer than the typical coda song. In the 3 remaining cases, they were 1.07 - 1.83 min shorter than the typical coda song.

When all songs emitted by male 8305 in 1983, 1984 and 1987 were compared across years, no differences were observed in total song duration (KW test, $p>0.05$ for all comparisons (Table 3-3b). Male 8305 sang an intermediate song in all three years, a typical coda song in 1984 and 1987, and a short coda song in 1983 and 1987. There were no between-year differences in total duration of these specific songs (KW or MWU test, $p>0.05$ for all comparisons; Table 3-3b)

When all songs emitted by male 8805 in 1988 and 1989 were compared between years, total song durations were longer in 1988 (MWU test, p=0.008, n=171, 230). Intermediate, short, typical, and long coda songs were sung in both years. Short coda songs recorded in 1988 were longer (MWU test, p=0.02, n=13, 15; Table 3-3b), while long coda songs recorded in 1988 were briefer than in 1989 (MWU test, p=0.04, n=22, 22). There were no between-year differences for intermediate songs and typical coda songs.

3.3.4 Breathing patterns and variability in the amount of time spent underwater

The mean number of breaths taken during the surface portion of a song varied from 5.2 to 8.2 (grand mean 6.5, SD=0.91, n=23). The mean proportion of time spent at the surface by each male varied from 0.16 to 0.42 (grand mean 0.27, SD=0.06, n=23). For those males singing alone with only faint or moderately loud background vocalizations, the mean number of breaths taken at the surface was positively correlated with the mean time spent underwater (Spearman, $p=0.003$, $n=23$). The number of breaths taken at the surface was positively correlated with time spent underwater in 11 of 23 males (Spearman, $p<0.05$ for all tests).

3.3.5 Factors affecting the frequency of occurrence and the duration of songs

The length of singing bouts

It was not possible to establish a seasonal singing profile for any one male. However, most mature males sang continually for many hours at a time, and in some cases, for 2 or 3 days. Male 8805 was observed in the study area for 27 days in 1988. During that time he sang for 197 hrs in 8 singing bouts that ranged in duration from 8 to 43 hr ($\bar{x}=23.89$, SD=10.82). One bout may have been as long as 65 hrs. Figure 3-6 summarizes the periods of time he sang and when he was silent. During one silent period he was observed hauled out along the edge of the polynya approximately 1.0 to 1.5 km from where he had been singing the previous day. Although the data base on other males is not as complete, long singing bouts were recorded for 11 other walruses (Table 3-6).

I examined differences in the frequency of occurrence and in the total duration of songs in four of the singing bouts emitted by male 8805. In all cases the occurrence of certain songs varied depending on whether it was the beginning, middle or end of the bout (Table 3-7a). In 3 of 4 cases, the occurrence of coda songs decreased while intermediate and aberrant songs increased as the bout progressed; however, in one instance the trend was the opposite. Total song duration varied throughout the bout in 2 of 4 cases; in one bout songs gradually became longer and in the other they became shorter (Table 3-7b).

Recording date

Multiple recordings were obtained from six males singing alone with only faint or moderately loud background vocalizations. Two of the males, 8305 and 8805, were recorded in more than one year, making it possible to examine the effects of recording date in up to 8 different cases, when sample sizes were adequate. The spread between recording dates for each male ranged from 3 to 45 days ($\bar{x}=18.0$ $SD=13.7$), and all males except 8305 (in 1983) and 8502 were recorded three times. The occurrence of each song type or variation emitted varied with date in 5 of 6 cases that could be tested (G-tests; $p<0.05$ for all comparisons; Table 3-8a). Except for male 8903, and possibly male 8907, there was little evidence to suggest that songs changed progressively from early to late in the season. Male 8903 was recorded five times. The incidence of short codas decreased slightly over the first three recordings, but then increased sharply for the last two. Male 8907 was recorded three times; the second and third recordings contained much higher proportion of erratic coda songs and fewer short coda songs.

The total duration of each male's songs varied with date in 2 of 8 cases (Table 3-8b). Male 8903 progressively shortened his songs throughout the season (KW test, $p<0.001$, Tukey tests, $p<0.05$). Male 8805 (recorded in 1988) emitted his longest songs in mid season (KW test $p<0.001$, Tukey tests $p<0.05$). Songs of 8805 (recorded in 1989) did not vary with date. Although male 8907 was recorded over a 25-day period, and there was a significant shift in proportion of song types over that period, the total durations of his songs did not vary.

Age and dominance status

Males recorded in this study were divided into three groups based on their relative age and dominance status: mature males > 15 years of age that were known to have attended a herd of females (Attending Males); mature males > 15 years of age that were never observed to attend a herd of females (Mature Males); and males 10-15 years of age that were never observed to attend a herd of females (Young Adult Males). The frequency of occurrence of songs and the number of breaths taken at the surface varied significantly relative to age and dominance status of the male; total song durations and the proportion of time spent underwater did not (Tables 3-9a, 3-9b, and 3-9c). Small sample sizes hampered analyses.

Attending Males recorded in 1988 sang almost exclusively DV songs while most other males (Young Adult Males and Mature Males combined) predominantly sang coda-song variations (Table 3-9a). A comparison between the proportion of DV songs and the proportion of all "other" song types and variations combined by male, showed that Attending Males emitted a greater number of DV songs (MWU test, $p=0.04$, $n=2, 8$) and fewer "other" songs (MWU test, $p=0.002$, $n=2, 8$) that other males. In 1989, Attending Males and Young Adult Males sang a greater number of short coda songs compared with Mature Males (KW test, $p=0.01$; Tukey test, $p<0.05$ $n=3, 4, 4$; Table 3-9b). In 1989, song repertoires of Young Adult Males were more similar to the Attending Males than to other Mature Males.

In 1988, there was no differences between the songs of Mature Males and Young Adult Males relative to total duration (MWU test, $p=0.82$, $n=4, 4$), proportion of time spent at the surface (MWU test, $p=0.49$, $n=4, 4$), or number of breaths taken at the surface (MWU test, $p=0.99$, $n=4, 4$). It was not possible to include Attending Males in these analyses for two reasons. First, both attending males emitted exclusively DV songs and the rest of the males mainly emitted coda songs. Since there can be significant differences in the duration of coda and DV songs it was not possible to separate age or dominance status effects from a possible song-type effect. Secondly, one of the attending males was only recorded while singing near females, which further confounds data interpretation (see next section). However, data for the two attending males are summarized in Table 3-9c for comparison. In 1989, songs did not differ among the 3 groups of males relative to total duration (KW test, $p=0.07$, $n=4, 3, 4$) or proportion of time spent at the surface (KW test, $p=0.70$, $n=4, 3, 4$). However, Mature Males took more breaths at the surface than either Attending Males or Young Adult Males (KW test, $p=0.03$, Tukey test, $p<0.05$, $n=4, 3, 4$).

Social context

Most males in this study were recorded while singing alone, but five were recorded during other circumstances. Male 8903 sang alone, when a silent male was nearby, when other mature males were singing intermittently within 100 m of him, and when he was attending a herd of females. Males 8907 and 8910 were recorded singing under similar conditions, though neither of them was accompanied by a silent male on a regularly basis. Instead, the analysis included songs recorded when these males were within 100 m of a small herd of females and calves, but were not interacting with them directly (i.e., they were not attending males). Male BR04 was recorded while singing at a hole in the ice beside a mature male that had been drugged and was being fitted with a VHF radio tag, at a hole directly in front of a herd of young adult males, and when he was an attending male. Male BR02 was recorded alone and when he sang and briefly interacted with a female and her calf.

All five males sang their longest songs when they were alone and their shortest songs when there were females in the immediate area (KW test, $p<0.0005$; Tukey test, $p<0.05$, for each male; Table 3-10a and b). Three of the 5 males spent a larger portion of time at the surface when they were singing near females compared to when they sang alone or when other males were in the area (KW test, $p<0.003$; Tukey test, $p<0.05$, for each male; Table 3-10a and b). Four of the males emitted short, typical and erratic coda songs and each significantly varied the frequency of occurrence of these songs in relation to social context. A greater number of short and erratic coda songs, and fewer typical coda songs, were emitted when males sang in the vicinity of females (G-tests, $p<0.05$ for all comparisons Table 3-11a). Male BR02 emitted DV songs, and although it is not certain that a consistent short version of this song exists, he sang the full song when alone and a consistent short variation (sequences III, IV and V were omitted) when he was the attending the herd of females (G-test, $p<0.05$; Table 3-11b).

3.4 DISCUSSION

3.4.1 Variability in the structure and organization of walrus songs

Underwater recording of 23 mature male Atlantic walruses, made in a number of different social contexts, confirms that walrus songs are generally consistent within and among individuals frequenting a polynya (Ray and Watkins 1975; Stirling et al. 1983, 1987). Nineteen out of 23 males sang coda song variation or DV songs at least 75% of the time. The basic structure and total duration of a typical coda and DV song have not changed since 1983 (Stirling et al. 1983, 1987; this study). Stirling et al. (1987) noted that shorter and longer coda songs, and shorter DV songs sometimes occurred, but did not recognize them as consistent song variations.

Earlier research on walrus vocal behavior focused on the surprisingly consistent nature of songs and did not address variation. In addition to DV songs, typical, short, and long coda songs, males also emit an erratic coda song, an intermediate song, and an aberrant song. These differ from the previously mentioned DV and coda songs in that they are often not individually consistent and the exact structure and organization of each song is not shared by all males frequenting the Dundas Island polynya. This is particularly true for the aberrant songs. In 19 of 23 males, intermediate, aberrant, and erratic coda songs constituted 0 to 25% of their repertoire; for the remaining 4 males this proportion reached a maximum of 43%. Given the larger sample of males and songs in the sample, this variability is not surprising and does not seriously alter the conclusions earlier studies which have emphasized consistency. However, these data show that less consistent songs are also a component of some males' song repertoire.

Because walruses breed and sing during the winter in areas of relatively inaccessible habitat, opportunities to record their songs are limited, and few recordings are available for comparative purposes. Ray and Watkins (1975) observed and recorded a male Pacific walrus, *O.r. divergens*, for five hours during March in the Bering Sea. Based on the information presented by the authors, it appears the composition and order of the underwater sequences emitted by this male differs markedly from any of the songs described here. The overall song structure is most similar to the short coda song. Durations of 15 songs emitted by the male averaged 2.40 min long, which is briefer than any of the songs recorded at the Dundas Island polynya. Another isolated observation on the surface/dive times (no recordings were made) of three male Pacific walruses singing near a herd of females indicated their songs were also approximately 3 min long (Fay et al. 1984). The possible significance of these brief songs is discussed in more detail later.

The only other marine mammal species that has a vocal display similar to the walrus, is the humpback whale, *Megaptera novaeangliae*. Compared to walrus songs, whale songs have longer durations and are composed of a greater variety of acoustically complex sounds. Nevertheless, there are some interesting structural similarities (Payne and McVay 1971; Payne et al. 1983). In humpback whale songs individual sounds are called units; several units are combined into a phrase; several phrases sung in a particular order compose a theme; and each song has several themes sung in a specific order (Payne and McVay 1971; Payne et. al. 1983). In walrus songs, the individual knocks and taps could be considered analogous to units, and the knocking and tapping series that compose a sequence analogous to phrases and themes, respectively. In songs of both species, the order in which themes and sequences are emitted appears to be consistent. The exacting structure of humpback whale song may facilitate learning of the complex song. Phrases and themes that are repeated at certain points in the song may help "remind" the whale of what comes next (Payne 1991). A similar interpretation may apply to walrus songs.

3.4.2 Factors influencing the frequency of occurrence and duration of walrus songs

A male's relative age and social status, social context, duration of singing bouts, and date of recording date all appear to influence the frequency of occurrence of songs and song duration. The most important factor appeared to be the presence of females near the singer. Males that were recorded in several different social contexts significantly shortened the total duration of their songs, emitted relatively more short coda songs, and spent more time at the surface when they were attending males or were singing near females, compared to when they sang alone.

There are at least two reasons why males might vary their songs while attending a herd or while singing near females. Silent, young adult males associating with the herd often approach female herd members as soon as the attending male dives underwater to sing the underwater portion of his song. Occasionally these younger males have time to initiate courtship behavior and, on rare occasions, a partial mount (Chapter 2). Just before the attending male surfaces, the young adult male moves several meters away from the female. The attending male may shorten his song and spend more time at the surface, to minimize the possibility of interactions between younger males and females. Shortening the song also means that the number of full songs emitted per hour would increase, and that surface codas and DV vocalizations would be heard more often. Given that surface codas (Chapter 3), and possibly diving vocalizations (Stirling et al. 1987), convey information on the identity of a male, short songs may allow an attending male to reinforce or advertise his identity. These two factors may also explain why the songs of Pacific walruses are so brief. A higher incidence of male-male aggressive interactions may intensify the need for short songs in Pacific walruses (Chapter 2).

The relationship of relative age and social status to the proportion of song types and variations emitted and to song duration could not be confirmed due to small sample sizes. However, in 1989, there appeared to be more similarities in the frequency of occurrence and total song duration between the songs of Young Adult Males and Attending Males than there were between Mature Males and Attending males. The reasons for this are not clear, but there are at least two possibilities. If a mature walrus greater than approximately 15 years of age has not successfully established himself as a high-ranking male, there may be less incentive for him to sing in a particular way. At least some of young adult males still have a chance to become dominant and the pressure of this competition may be reflected in their singing behavior.

It was difficult to identify seasonal trends in the frequency of occurrence of songs or song duration because few males were recorded more than once in comparable social contexts. Male 8903 sang relatively few short coda songs for most of the season, then sharply increased the number near its end; male 8907 emitted a high proportion of erratic coda songs during the last half of the season. For male 8903, it is questionable whether the trend was seasonal or related to more interactions with females. As the season progressed, this male spent more time attending females and singing short coda songs; by the end of the season, this shift in song variation may have carried over to times when he was singing alone. Based on available data, male 8907 did not spend more time with females as the season progressed; therefore, the increase in erratic coda songs late in the season may reflect a seasonal trend for this male. In general, however, it appears that seasonal effects are minor and perhaps masked by other factors. There is little evidence of a seasonal trend in song duration. Only 2 of 8 males varied song duration with recording date; male 8903 progressively shortened his songs throughout the season while 8805 (recorded in 1989) sang his longest songs at mid season. Results for 8903 are consistent with what would be expected given short coda songs are shorter than typical coda songs. It is difficult to interpret the results for 8805; there was no obvious explanation for the long song during the mid season recording.

There were several between-year shifts in the proportions of song types and variations emitted. A greater number of typical coda songs and fewer DV songs were recorded in 1989, compared with 1988. Stirling et al. (1987) also documented a strong difference in proportions of certain songs between years. Although results of the two studies are not directly comparable because the earlier study included strum songs, and did not categorize coda songs into short, typical, and long variations, it appears that year-to-year changes in proportions of song types and variations occur regularly. However, it is not apparent why.

One possibility is that shifts occur when new males move into the polynya. For this explanation to be plausible, individual males would have to show a strong and consistent preference for a particular song type or variation. Existing data indicate that this is not always true. Many, if not all, mature males frequenting the polynya can sing all major song types and variations (Stirling et al. 1987; this study). In addition, some males change the proportions of song types and variations significantly between years. Male 8805 sang more typical coda songs and fewer DV songs in 1989, compared with 1988. More importantly, this shift generally reflected what other males in the polynya were singing, which suggests that males imitate one another. Perhaps if the most dominant males in the polynya are singing coda songs, other males may do so. There is some support for this idea; in 1989, the four attending males all sang variations of the coda song and so did all other males (virtually no DV songs were recorded in that year). In 1988, the 2 attending males emitted exclusively DV songs, and 3 of the remaining 8 males sang DV songs exclusively or part of the time. There is considerable evidence for song learning, song matching and mimicry in birds (Falls 1982). Almost all oscine bird species that sing complex songs or have song repertoires learn them from other individuals. In most cases, the "tutor" is the father or another male that the young bird interacts with (Falls 1982; Kroodsma 1982). For example, Village Indigo birds, *Vidua chalybeata*, are polygynous and young males copy the songs of successful breeding males (Payne and Payne 1977; Payne 1981).

The length of a mature male walrus's singing bout is one of the longest, if not the longest, ever documented for a mammal (Winn and Winn 1978). These bouts are emitted on a regular basis for at least two months of the breeding season. The proportion of song types, song variations, and song duration vary depending on whether they were emitted near the beginning, middle or end of a singing bout. Male 8805 sang fewer coda songs and a greater number of intermediate and aberrant songs as the bout progressed. Results for song duration were difficult to interpret because of the small sample sizes. However, durations varied in 2 of 4 cases; on one occasion male 8805 gradually lengthened his songs and on the other he shortened them. Given the length of the singing bouts one might expect that fatigue or monotony could influence the occurrence of song types and variations and the duration of songs. Either of these factors would generate higher variation near the end of a singing bout. Data presented above support this prediction. In birds, it has been suggested that one function for a large repertoire of songs is to enhance the effectiveness of the display by decreasing monotony (Hartshorne 1956, 1973; Kroodsma 1978).

3.4.3 The function and evolution of walrus songs

Little is known about the function of walrus songs or the selective pressures that have shaped them. Ray and Watkins (1975) suggested that songs advertise the presence of a male in breeding condition, and perhaps to establish an underwater territory or dominance hierarchy. Observations on walruses in this study (Chapter 2) suggest that a male's singing ability helps to maintain his dominance status in the absence of fighting, and that intra-sexual selection has been important in song evolution. Males that sang most extensively were the ones that gained access to herds of females and calves. Young adult males in the immediate vicinity of a herd of females curtailed their singing activities in the presence of an attending male. All males had the opportunity to assess each other's singing capabilities for long periods because of the restricted access to open water and the stability of the sea ice in the area. Limited observations suggest that males respond to singing of other males (Chapter 2). Unfortunately, there are no data on whether certain aspects of a male's singing ability is related to fighting ability or some other aspect of body condition that may be closely linked to fighting ability. Observations of aggressive interactions involving physical contact between males were rare during the study. Without such data it is not possible to confirm whether songs function to maintain dominance relations. However, the low level of physical interactions suggest that singing performance is important for maintaining stable dominance relations in the absence of fighting.

There is less evidence to support the idea that male Atlantic walruses use their songs to establish an acoustic territory. The movements of female herds and attending males were wide-ranging and variable depending on tide, currents, water-surface conditions and ice conditions. Even when no females were visible, singing males move about the polynya and do not appear to defend a specific area. There is even less evidence to support the idea that songs function to attract females. It is difficult to reliably identify female walruses, so tracking their movements relative to singing males is not possible.

Even though there is little evidence to confirm that Atlantic walrus songs function to attract females, female preferences could be important. If some aspect of singing ability conveys information about a male's social status, females, like males, have ample opportunity to monitor and assess the songs of all males during the breeding season. They also have an opportunity to acquire information on the dominance status of each singer. In addition, lone females are probably capable of recognizing which males spend the most time attending large herds, based on the song types and variations being emitted (i.e., males sing a higher proportion of short coda and DV songs when attending a herd). Given this scenario, it is probably too simplistic to conclude that the functions of walrus song have been shaped only by intra-sexual selection. Relatively little is known about the function of humpback whale songs; however, Tyack (1981) suggests that they evolved in response to both intra- and inter-sexual selection. A number of studies of bird songs have also demonstrated that some species emit song types that have relatively distinctive intra- and inter-sexual functions (Baptista 1978; Payne 1979; Catchpole 1987; Kroodsma et al. 1987).

If males use singing behavior to assess their opponents' social status and potential fighting ability, or if females use singing to assess a male's fitness, then the assessment criteria must be closely linked to those traits; if not, cheating could occur (Maynard Smith and Price 1973; Parker 1974; Zahazvi 1975; Maynard Smith and Parker 1976; Zahavi 1977). In many species the vocal displays of males during the breeding season appear to be strenuous and energetically expensive (e.g., Clutton-Brock and Albon 1979; Taigen and Wells 1985; Wells and Taigen 1986; Robertson 1986). There are also a number of acoustic features in a vocal display that could serve as "copy proof" criteria of a males general body condition or size, for example, the fundamental frequency of the call in some species of birds and frogs (Davis and Halliday 1978; Morton 1977). To fully understand the function of walrus songs it will be necessary to identify what features males and females are listening to.

One such feature may be how long a male sings. Humpback whales sing complex songs that are repeated every 5 to 30 min, in bouts that can last for as long as 22 h (Winn and Winn 1978). Walruses sing songs that are repeated every 5 to 8 min, in bouts that commonly last 48 hours. There is good evidence that some males sing continuously for at least 65 hr. The length of time over which a male can sustain continuous singing may be both an accurate and reliable indicator of his general condition. Both male and female walruses have the opportunity to assess this feature of singing behavior. Attending males spent a longer time in the polynya and sang for longer periods of time than other males (Chapter 2). At the end of the breeding season in May, some of the largest and oldest males were noticeably emaciated. It was not possible to confirm if these emaciated males were the same ones that sang extensively during the peak of the breeding season, but it is quite likely that they were (scars used to identify males in the water are not visible when the male is hauled out). These observations suggest that a male's ability to sing continuously for long periods of time during the entire breeding season is linked to body condition, particularly fat reserves. Thus, the duration of a male's singing bout and the amount of recovery, or rest time between bouts may convey information about his general physical condition. Positive relationships among body condition, breeding performance and reproductive success have been documented for several species of land breeding pinnipeds (Le Boeuf 1972, 1988; Boness 1991; Deutsch 1990)

A number of factors other than sexual selection may have influenced the evolution of walrus songs. The dive pattern of a feeding walrus is remarkably similar to the dive pattern of a singing walrus during the breeding season. Feeding walruses dive for approximately 5 min and then remain at the surface for 1-2 min (Fay 1982). Data obtained by satellite telemetry show that they dive continuously for up to 21 hr/day for 2-4 days at a time (Erik Born, personal communication). At the end of the feeding bout they return to a land or ice haul-out site to rest for approximately 2-3 days. It is thought that elaborate communication signals arise from common behaviors that gradually evolve into ritualized and stereotyped displays (Tinbergen 1959; Alcock 1989). The courtship and mating displays of a variety of bird and insect species involve ritualized aspects of feeding behavior (e.g., Kessel 1955; Lindauer 1961; E.O. Wilson 1971). The striking similarities between the feeding dive pattern and singing dive pattern may be an example of this evolutionary process. If true, this would certainly validate the idea that a male's ability to sing for long periods of time with minimal recovery time between bouts is closely linked to his physical condition and foraging ability.

3.5 LITERATURE CITED

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Table 3-1. Summary of recording information for identified walruses.

Walrus identification	Date of first and last recording(d/m/y)	Number of days recorded	Number of recording sessions	Hours recorded
8305	13/04/83 18/04/83	2	2	2.0
8305	11/04/84 24/04/84	5	5	3.6
8305	04/03/87	1	1	4.7
8502	16/03/85 24/03/85	3	3	5.0
8607	09/04/86 27/04/86	3	5	7.8
8801	27/02/88	1	1	9.5
8802	02/03/88	1	1	2.4
8803	18/03/88 19/03/88	2	3	3.7
8804	19/03/88	1	1	3.4
8807	27/04/88	1	2	4.7
BR01	25/04/88	1	1	2.5
BR04	16/04/88 30/04/88	4	5	9.2
BR11	28/04/88 29/04/88	2	2	7.9
BR44	28/04/88	1	1	1.9
8805	19/03/88 15/04/88	7	10	24.0
8805	27/03/89 07/04/89	6	13	32.7
8901	11/02/89	1	1	1.6
8903	13/02/89 15/04/89	24	44	88.9
8904	17/02/89 23/03/89	3	3	8.6
8905	17/02/89 04/04/89	2	2	4.4
8906	20/02/89 27/02/89	3	4	10.5
8907	23/02/89 20/03/89	9	26	47.2
8908	12/02/89 20/04/89	5	9	20.8
8910	06/03/89 24/03/89	3	6	12.8
8912	25/02/89 13/04/89	5	6	9.0
BR02	19/02/89	1	1	5.6

Table 3-2. Between year-differences in the mean frequency of occurrence of songs emitted by walruses recorded in 1988 and 1989.

Song type or variation	1988 % n=10	1989 % n=11
Typical coda	32.9	57.0
Short coda	12.5	22.9
Long coda	8.5	4.5
Erratic coda	3.4	12.0
DV	30.2	0.04
Intermediate	0.8	0.04
Aberrant	14.4	3.5

Table 3-3a. Between-year differences in the frequency of occurrence of songs emitted by males 8805 and 8305.

Walrus identification	Song type or variation	Year		
		I	II	III
		1988	**1989**	
8805	Short coda song	8.1 (15/185)	6.2 (15/240)	
	Typical coda song	48.7 (90/185)	70.4 (169/240)	
	Long coda song	11.8 (22/185)	10.0 (24/240)	
	Intermediate	21.1 (39/185)	8.3 (20/240)	
	Other (aberrant; DV)	10.3 (19/185)	5.0 (12/240)	
		1983	**1984**	**1987**
8305	All coda songs	69.2 (9/13)	59.3 (16/27)	81.6 (31/38)
	Intermediate	23.1 (3/13)	29.6 (8/27)	13.2 (5/38)
	Other (Aberrant & DV)	7.7 (1/13)	11.1 (3/27)	5.3 (2/38)

Table 3-3b. Between-year differences in the total duration of songs emitted by 8805 and 8305.

Walrus identification	Song type or variation	Year		
		I	II	III
		1988	**1989**	
8805	Total song duration (all songs combined)	7.92 ± 1.50 (171)*	7.55 ± 1.99 (230)	
	Short coda song	6.64 ± 1.03 (13)	5.75 ± 0.97 (15)	
	Typical coda song	7.45 ± 0.98 (86)	7.41 ± 1.2 (164)	
	Long coda song	9.10 ± 0.65 (22)	9.74 ± 1.66 (22)	
	Intermediate song	8.07 ± 1.79 (39)	8.09 ± 2.17 (17)	
8305		**1983**	**1984**	**1987**
	Total song duration (all songs combined)	8.05 ± 1.78 (171)	7.89 ± 1.77 (24)	7.27 ± 1.51 (38)
	Short coda song	7.77 ± 1.01 (7)		6.63 ± 1.65 (13)
	Typical coda song		7.40 ± 1.5 (13)	7.37 ± 1.56 (17)
	Intermediate	8.02 ± 2.11 (3)	9.14 ± 1.47 (7)	8.28 ± 0.46 (5)

* mean ± SD (n)

Table 3-4. Summary of time at surface, and total durations for each song type/variation (1983 - 1988). In each cell, surface time is shown above total song duration ($\bar{x}$ ± SD).

Walrus identification	Short coda	Typical coda	Long coda	Erratic coda	DV	Intermediate coda	Aberrant
8801	1.00 ± 0.37 3.51 ± 0.77 n=38	1.37 ± 0.59 5.31 ± 0.87 n=34	1.57 7.683 n=1	0.86 5.13 n=1	1.59 ± 0.44 7.24 ± 0.68 n=13	1.64 ± 1.38 6.12 ± 2.57 n=8	2.01 ± 0.27 12.31 ± 4.64 n=6
8802	1.76 ± 0.40 4.61 ± 2.57 n=14	1.85 ± 0.50 5.56 ± 0.53 n=23		1.17 2.88 n=1			
8803	1.53 ± 0.13 6.27 ± 0.81 n=3	1.85 ± 0.57 7.19 ± 1.52 n=29	1.783 9.30 n=1				1.60 ± 0.10 6.13 ± 1.39 n=3
8804	2.15 ± 0.68 5.03 ± 0.52 n=9	1.98 ± 0.48 6.73 ± 1.05 n=18		1.71 ± 1.15 6.03 ± 2.33 n=3			1.28 5.07 n=1
8805	2.52 ± 0.60 6.64 ± 1.03 n=13	2.05 ± 0.54 7.45 ± 0.98 n=86	1.82 ± 0.45 9.10 ± 0.65 n=22		2.64 ± 0.82 9.01 ± 1.44 n=8	2.65 ± 0.95 8.07 ± 1.79 n=35	2.34 ± 0.65 10.88 ± 1.93 n=6
8807					1.04 ± 0.25 6.31 ± 1.1 n=41		1.19 ± 0.20 4.41 ± 0.63 n=2
BR01					1.76 ± 0.55 5.24 ± 0.91 n=27		
BR11		1.66 ± 0.65 8.27 ± 2.20 n=10	1.36 ± 0.14 8.99 ± 0.97 n=34	1.32 ± 0.24 8.20 ± 2.64 n=3			
BR44	1.20 3.68 n=1	1.33 ± 0.53 5.01 ± 1.18 n=3	1.42 5.23 n=1	1.49 ± 0.55 4.24 ± 1.24 n=3		1.38 6.35 n=1	1.48 ± 0.44 7.57 ± 1.90 n=9

Walrus identification	Short coda	Typical coda	Long coda	Erratic coda	DV	Intermediate coda	Aberrant
8305 (1983)	2.51 ± 1.02 7.77 ± 1.01 n=7	3.66 ± 1.66 10.38 ± 2.11 n=2		0.95 5.42 n=1		3.42 ± 2.02 8.02 ± 2.11 n=3	
8305 (1984)	1.58 ± 0.65 5.49 ± 1.24 n=2	2.08 ± 1.25 7.40 ± 1.50 n=13		1.57 8.18 n=1		2.36 ± 0.17 9.14 ± 1.47 n=7	4.72 10.17 n=1
8305 (1987)	1.65 ± 0.27 6.63 ± 1.65 n=13	1.76 ± 0.61 7.37 ± 1.56 n=17	1.45 7.43 n=1		2.07 8.25 n=1	1.89 ± 0.50 8.28 ± 0.46 n=5	
8502		1.14 ± 0.42 5.46 ± 0.88) n=18		1.22 ± 0.32 6.02 ± 1.43 n=25			
8607	1.50 ± 1.00 3.40 ± 1.00 n=4	1.44 ± 0.58 4.73 ± 0.66 n=17	1.08 ± 0.25 5.52 ± 0.58 n=3	1.20 ± 0.33 4.45 ± 1.05 n=9	1.42 ± 0.45 5.29 ± 0.88 n=20	1.67 ± 0.56 5.32 ± 0.65 n=10	1.69 ± 0.52 8.22 ± 2.89 n=5

Table 3-5. Summary of time spent at surface, and total durations for each song type/variation (1989). In each cell, surface time is shown above total song duration (x̄ ± SD).

Walrus identification	Short coda	Typical coda	Long coda	Erratic coda	DV	Intermediate coda	Aberrant
8805	1.71 ± 0.39 5.75 ± 0.97 n=15	1.77 ± 0.52 7.41 ± 1.20 n=164	1.94 ± 0.51 9.74 ± 1.67 n=22	1.36 ± 0.65 5.35 ± 4.08 n=5	2.50 8.07 n=1	1.81 ± 0.55 8.09 ± 2.17 n=17	2.70 ± 0.69 5.58 ± 3.53 n=3
8901	3.05 5.00 n=1	2.74 ± 0.94 6.50 ± 1.153 n=9	3.14 ± 0.64 8.36 ± 0.88 n=3				
8903	1.53 ± 0.53 5.15 ± 1.125 n=243	1.64 ± 0.49 6.93 ± 1.12 n=437	2.01 ± 0.91 7.26 ± 0.28 n=3	1.91 ± 1.75 6.11 ± 3.60 n=95			2.28 ± 0.82 8.02 ± 4.08 n=3
8904	1.10 ± 0.45 2.27 ± 0.58 n=13	1.22 ± 0.43 4.29 ± 0.53 n=43	1.34 ± 0.81 5.66 ± 0.83 n=6	1.23 ± 0.46 4.30 ± 1.23 n=19			1.23 ± 0.74 6.45 ± 1.50 n=7
8905	1.16 ± 0.40 3.30 ± 0.90 n=10	1.09 ± 0.33 4.47 ± 0.83 n=26	1.40 ± 0.19 6.16 ± 0.95 n=5	1.04 4.10 n=1			
8906	2.23 ± 0.38 8.33 ± 0.99 n=6	2.51 ± 0.91 9.53 ± 1.91 n=46	2.45 10.53 n=1	2.39 ± 1.23 8.57 ± 2.46 n=5			
8907	0.91 ± 0.42 4.69 ± 1.88 n=206	0.99 ± 0.32 6.04 ± 1.47 n=85	1.34 ± 0.57 7.97 ± 4.23 n=4	1.06 ± 0.32 6.05 ± 2.32 n=189			
8908	1.92 ± 0.62 5.00 ± 1.09 n=73	1.84 ± 0.64 6.35 ± 1.10 n=81	1.53 ± 0.30 7.65 ± 1.11 n=7	1.77 ± 0.64 6.24 ± 2.08 n=26		2.22 9.37 n=1	1.74 ± 0.58 7.54 ± 1.30 n=6
8910	0.87 ± 0.34 3.22 ± 0.95 n=80	1.08 ± 0.42 4.48 ± 1.02 n=82		1.39 ± 0.49 4.93 ± 0.84 n=13			

Walrus identification	Short coda	Typical coda	Long coda	Erratic coda	DV	Intermediate coda	Aberrant
8912	1.34 ± 0.48 5.77 ± 0.84 n=19	1.57 ± 0.55 7.29 ± 1.16 n=55					
BR02	0.93 ± 0.39 3.03 ± 0.60 n=16	1.31 ± 0.25 4.60 ± 0.51 n=52		2.14 4.98 n=2			

Table 3-6. Summary of song-bout durations.

Walrus identification	Date (d/m/y)	Duration of singing bout (hrs)
8805	27/03/89	8
	31/03/89	8
	6-7/04/89	41
8907	23-26/02/89	57
	11/03/89	11
	17-20/03/89	81
8908	11/04/89	14
	17/04/89	8
	20/04/89	13
8910	24/04/89	8
8912	07/03/89	12
8903	13/03/89	10
	14/03/89	10
	25-26/03/89	33
	05/04/89	21
8801	27/02/88	10
8807	27/04/88	8
BR04		16
BR11	28-29/04/88	18
8502	16/03/85	14
	19/03/85	15
	20/03/85	21
	24/03/85	17
8607	27/04/86	13

Table 3-7a. The relationship of frequency of occurrence of songs to location in song-bout (male 8805 in 1988 and 1989).

Date	Song type or variation	Location in bout			G-test Statistic
		Beginning	Middle	End	
		1-7 hrs	**8-15 hrs**	**16-31 hrs**	
19-21/03/88	Short coda	40.0 (8/20)	24.1 (7/29)	0	G = 13.272
	Typical coda	25.0 (5/20)	44.8 (13/29)	50.0 (9/18)	p = 0.010
	Other*	35.0 (7/20)	31.1 (9/29)	50.0 (9/18)	
		1-3 hrs		**9-16 hrs**	
01-02/04/88	All coda songs**	20.0 (4/20)		77.0 (10/13)	G = 10.926
	Other	80.0 (16/20)		23.0 (3/13)	p = 0.001
		1-3 hrs	**8-14 hrs**	**20-24 hrs**	
14-15/04/88	Typical coda	57.9 (11/19)	85.7 (18/21)	31.3 (5/16)	
	Long coda	31.6 (6/19)	14.3 (3/21)	37.5 (6/16)	G = 15.443
	Other	10.5 (2/19)	0	31.2 (5/16)	p = 0.004
		1-7 hrs	**17-19 hrs**	**37-41 hrs**	
06-07/04/89	All coda songs	100.00 (25/25)	88.9 (16/18)	64.3 (18/28)	G = 21.241
	Other	0	11.1 (21/18)	35.7 (10/28)	p = 0.001

* Other = intermediate, DV, erratic coda and aberrant songs combined.

** All coda songs = short, typical and long coda songs combined.

Table 3-7b. The relationship of song duration to location in song-bout (male 8805 in 1988 and 1989).

Date	Location in bout			KW or MW-U Test results
	Beginning	Middle	End	
19-21/03/88	**1-7 hrs** 6.89 ± 0.97* a**	**8-15 hrs** 7.33 ± 1.46	**16-31 hrs** 8.48 ± 2.08 a	p= 0.0230
1-2/04/88	**1-3 hrs** 8.95 ± 1.86		**9-16 hrs** 8.22 ± 0.97	NS
14-15/04/88	**1-3 hrs** 8.11 ± 1.03	**8-14 hrs** 7.45 ± 1.05	**20-24 hrs** 8.11 ± 1.96	NS
6-7/04/89	**1-7 hrs** 7.72 ± 1.51 a	**17-19 hrs** 6.97 ± 1.51 b	**37-41 hrs** 5.10 ± 1.42 ab	p= 0.0001

* mean song duration ± SD

** Matching letters indicate significant multiple-pairwise comparisons within a song-bout.

Table 3-8a. The relationship of the frequency of occurrence of songs to recording date. All walruses were recorded singing alone. Each cell entry shows recording date, sample size and percent of each song type/variation in sample.

Walrus identification	Song type or variation	Date and number of recordings made				
		I	II	III	IV	V
		18/02/89	**27/02/89**	**24/03/89**	**08/04/89**	**15/04/89**
		n=12	n=20	n=12	n=16	n=25
8903	Short coda	16.7	10.0	0	56.3	48.0
	Typical coda	83.3	90.0	100.0	43.7	52.0
		24/02/89	**11/03/89**	**19/03/89**		
		n=71	n=39	n=43		
8907	Short coda	56.3	30.8	16.3		
	Typical coda	23.9	2.6	20.9		
	Erratic coda	19.7	66.7	62.8		
		19/03/88	**01/04/88**	**14/04/88**		
		n=71	n=44	n=70		
8805	Short coda	21.1	11.4	24.3		
(1988)	Typical coda	40.9	40.9	61.4		
	Intermediate	26.8	29.6	10.0		
	Aberrant	11.3	18.2	4.3		
		09/04/86	**24/04/86**	**27/04/86**		
		n=13	n=18	n=44		
8607	All coda songs	0	61.1	29.6		
	DV Song	38.5	0	34.0		
	Other	61.5	38.9	36.4		
		16/03/85	**19/03/85**			
		n=38	n=36			
8502	Short coda	0	11.1			
	Typical coda	42.1	38.9			
	Erratic coda	57.9	50.0			

Table 3-8b. The relationship of song duration to date. All walruses were recorded singing alone. Each cell entry shows recording date, mean song duration (in min), standard deviation and sample size.

Walrus identification	Date and number of recordings made				
	I	II	III	IV	V
8903	18/02/89 9.01 ± 2.90[*] abc[**] n=15	27/02/89 7.50 ± 0.81 bd n=19	24/03/89 6.64 ± 0.93 n=12	08/04/89 6.04 ± 0.84 cd n=14	15/04/89 6.00± 1.35 a n=26
8805 (1988)	19/03/88 7.52 ± 1.62 a n=63	01/04/88 8.55 ± 1.45 a n=41	14/04/88 7.91 ± 1.27 n=67		

[*] mean ± SD

[**] Matching letters indicate significant multiple-pairwise comparisons within an individual and across date.

Table 3-9a. The relationship of relative age and social status to the mean frequency of occurrence of songs emitted by walruses in 1988.

Song type or variation	Attending Male (%) n=2	Mature Male (%) n=4	Young Adult Male (%) n=4
Short coda	0	20.9	8.4
Typical coda	0	53.4	29.0
Long coda	0	3.8	17.5
Erratic coda	0	1.2	7.3
Intermediate	0	1.8	0
DV	96.4	4.8	23.4
Aberrant	5.4	12.1	14.4

Table 3-9b. The relationship of relative age and social status to the mean frequency of occurrence of songs emitted by walruses in 1989.

Song type or variation	Attending Male (%) n=3	Mature Male (%) n=4	Young Adult Male (%) n=4
Short Coda	29.9	8.7	21.8
Typical Coda	48.0	75.2	55.3
Long Coda	0.4	8.6	3.5
Erratic Coda	21.3	3.0	46.1
Intermediate	0	0.1	0
Other (dv, aberrant)	0.4	4.3	5.2

Table 3-9c. The relationship of relative age and social status to song duration, number of breaths taken at the surface and percent of time spent at the surface.

Year	Song variable	Attending Male	Mature Male	Young Adule Male
1988	Mean song duration ± SD	6.42 ± 1.98	6.38 ± 1.36	6.77 ± 1.35
	Mean breaths ± SD	7.2 ± 0.96	6.9 ± 1.20	6.8 ± 0.93
	Mean % time at surface	27.4	28.5	23.1
	N (number of males)	(2)	(4)	(4)
1989	Mean song duration ± SD	5.37 ± 1.02	7.90 ± 1.30	5.23 ± 1.44
	Mean breaths ± SD	5.9 ± 0.58 a	7.8 ± 0.22 ab	5.7 ± 0.60 b
	Mean % time at surface	24.4	30.8	26.3
	N (number of males)	(3)	(4)	(4)

** Matching letters indicate significant multiple-pairwise comparisons within a year and across male categories.

Table 3-10a. Relationship of social context to total song duration, number of breaths at surface and proportion of time at surface.

Walrus identification	Song variable	Singing alone; background songs faint-moderate	Singing alone; background songs loud; 8908 present	Singing alone; background songs loud and satellite male nearby	Singing alone; background songs moderate and females in area but not interacting with singing male	Attending male
8903	Mean song duration ± SD(n)	6.87 ± 1.88 (96) a**	7.01 ± 1.71 (61) b	6.37 ± 1.49 (137)		6.05 ± 1.90 (189) ab
	Mean no. breaths ± SD(n)	5.8 ± 1.2 (99) b	6.0 ± 1.02 (66)	6.0 ± 1.18 (148) a		7.0 ± 1.51 (189) ab
	Mean % time at surface	22.9% (96) a	24.8% (61)	26.4% (137) b		29.1% (189) ab
8910		5.16 ± 0.88 (37) abc		4.36 ± 1.11 (31) ade	3.64 ± 0.78 (17) bd	3.64 ± 0.78 (53) ce
		5.3 ± 0.76 (38)		5.1 ± 1.30 (32)	4.0 ± 0.82 (4)	5.4 ± 1.08 (36)
		26.4% (37)		26.5% (31)	24.4% (17)	26.9% (53)
8907		6.85 ± 1.73 (108) abc		5.97 ± 2.03 (181) ade	3.95 ± 1.25 (37) bd	3.71 ± 1.56 (97) ce
		6.0 ± 1.22 (115)		5.5 ± 1.15 (186)	6.2 ± 2.41 (37)	5.8 ± 2.15 (102)
		15.1% (108) abc		17.6% (181) ade	27.6% (37) bd	26.5% (97) ce
BR02		4.43 ± 0.76 (47) a				3.49 ± 0.86 (16) a
		6.6 ± 0.88 (46)				6.5 ± 1.41 (15)
		28.2% (47)				31.8% (16)

** Matching letters indicate significant multiple-pairwise comparisons within an individual and across social contexts.

Table 3-10b. The relationship of social context to total song duration, number of breaths at surface, and proportion of time at surface for BR04 in 1988.

Song variable	Singing alone in hole near drugged male	Singing alone in front of a herd of immature males	Singing as an attending male
Mean song duration ± SD (n)	10.52 ± 2.26 (7) a**	8.10 ± 1.60 (11) b	5.44 ± 1.16 (25) ab
Mean breaths ± SD (n)	7.4 ± 2.6 (9)	7.5 ± 2.03 (13)	6.7 ± 1.35 (27)
% time at surface	16.1% (7) a	15.1% (11) b	21.8% (25) ab

** Matching letters indicate significant multiple-pairwise comparisons across social contexts.

Table 3-11a. The relationship of social context to the frequency of occurrence of short, typical and erratic coda songs in 1989.

Walrus identification	Song variation	Singing alone; background songs moderate	Singing alone; background songs loud; 8908 present	Singing alone; background songs loud; satellite male nearby	Singing alone; background songs moderate; females nearby but not interacting with singer	Attending male
8903	Short coda	26.5 (26/98)	18.5 (12/65)	36.2(51/141)		38.5 (75/195)
	Typical coda	68.4 (67/98)	69.2 (45/65)	56.0(79/141)		45.3 (88/195)
	Erratic coda	5.1 (5/98)	12.3 (8/65)	7.8(11/141)		16.4 (32/195)
8910		2.8 (1/36)		37.5 (12/32)	47.1 (8/17)	81.4 (35/43)
		75.0 (27/36)		43.7 (14/32)	52.9 (9/17)	18.6 (8/43)
		22.2 (8/36)		18.8 (6/32)	0	0
8907		47.3 (52/110)		29.5 (56/190)	42.9 (18/42)	61.9 (65/105)
		14.5 (16/110)		21.1 (40/190)	14.3 (6/42)	5.7 (6/105)
		38.2 (42/110)		49.4 (94/190)	42.9 (18/42)	31.4 (34/105)
BR02		13.0 (6/46)				62.5 (10/16)
		87.0 (40/46)				25.0 (4.16)
		0				12.5 (2/16)

Table 3-11b. The relationship of social context to the occurrence of typical and short variations of the DV song (in percent) emitted by BR04 in 1988.

Song Variation	Singing alone in hole near drugged male n=9	Singing in front of a herd of immature males n=14	Singing as an attending male n=28
Full DV song	77.8	35.7	3.6
Short DV song	22.2	64.3	96.4

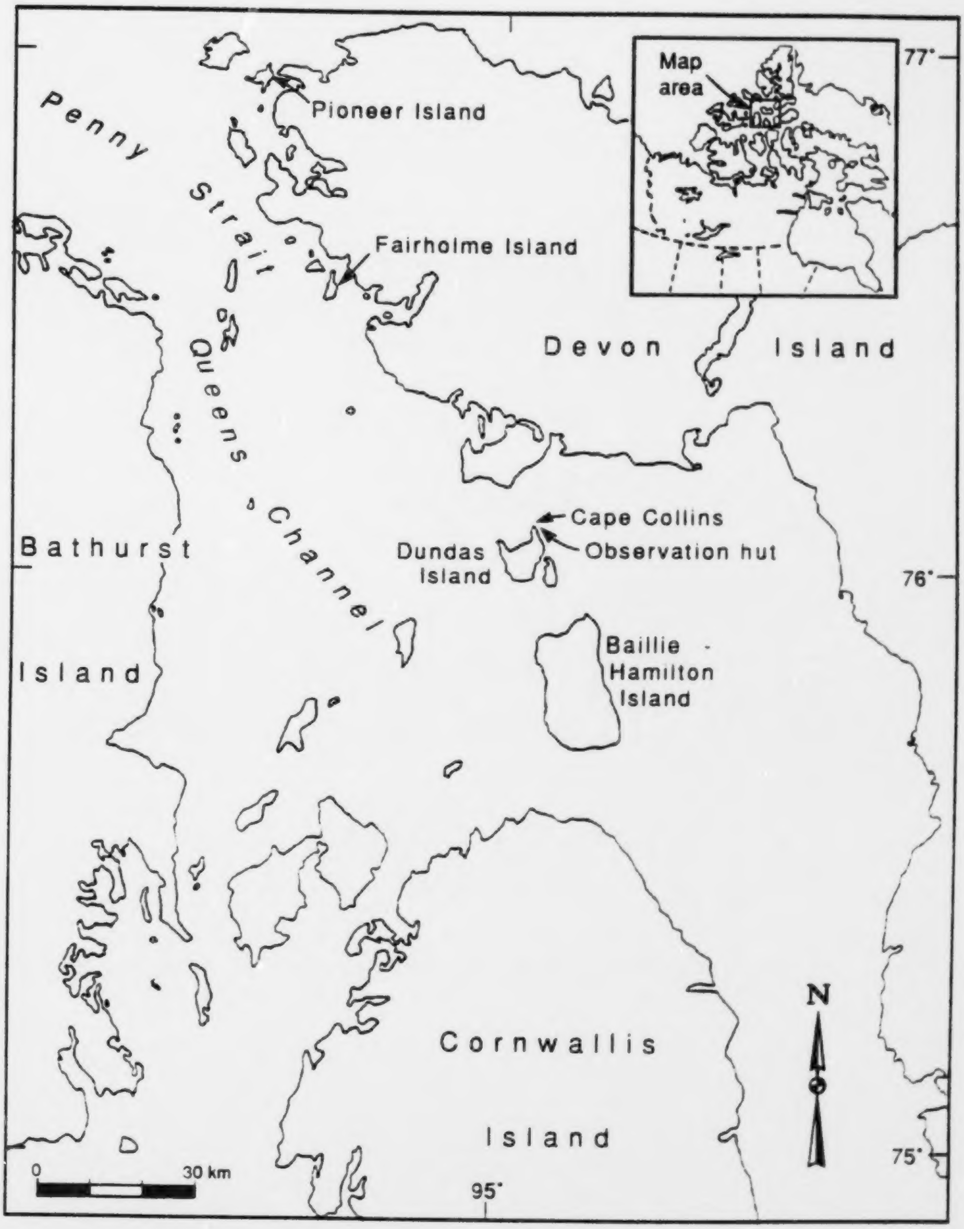
Map area
Penny Strait
Pioneer Island
Fairholme Island
Queens Channel
Devon Island
Bathurst Island
Cape Collins
Observation hut
Dundas Island
Baillie - Hamilton Island
Cornwallis Island
N
0
30 km
95°
77°
76°
75°

Figure 3 - 1. Map of the study area.

	Typical Coda Song	Diving Vocalization Song	Intermediate Song
Surface Portion	1) k 4k breath	1) k k breath	k 4k breath
	2) k 4k -- ts -- surface coda breath	k k breath	k 4k -- ts -- coda breath
	k 4k breath	k k breath	k 4k breath
	k 4k -- ts -- surface coda breath	k k t breath	k 4k -- ts SWITCH -- 2k breath
	k 4k breath	2) k -- ts -- 2k breath	k k breath
	k k walrus dives	k k walrus dives	k k walrus dives
Underwater Portion	I Long ks -- bk -- bkc	I dv -- long ks with two changes of pace -- bk	I Long ks -- with two changes of pace -- bk
	II 2t -- ks -- dk - bk	II 4t -- long ks -- dk - bk (pause of 5 - 15 s) bk	II 4t -- long ks -- dk - bk (pause of 5 - 15 s) bk
	III bk -- long, fast ts -- k - bk -- long ks -- bkc	III long ks -- 2k	III long ks -- SWITCH -- bkc
	IV 3t -- short ks -- series of bks -- 2k walrus surfaces and song is repeated	IV 2k -- long, fast ts -- k - strum	IV 2t -- ks -- dk - bk
		V 4t -- long, fast ts -- k - strum	V bk -- long, fast ts -- k - bk -- long ks -- bkc
		VI short ks -- tk walrus surfaces and song is repeated	VI 3t -- short ks -- 2k walrus surfaces and song is repeated

Figure 3 - 2. Schematic representation of a typical coda song, a diving vocalization (dv) song, and an example of an intermediate song. In the intermediate song two common types of switches are shown. The song switches from coda to dv in the surface portion and then in the third underwater sequence there is a switch from dv back to coda. Summary of abbreviations used: bk, bell-knock; dk - bk, double-knock bell-knock; bkc, bell-knock coda; k-strum, knock strum; ks, knocking sequence; ts, tapping sequence; k, single knock which is distinctive; t, single tap which is distinctive; 2k, two knocks which are easily recognized as a couplet; tk, triple-knock; dk, double-knock; and --, separable series of knocks and taps.

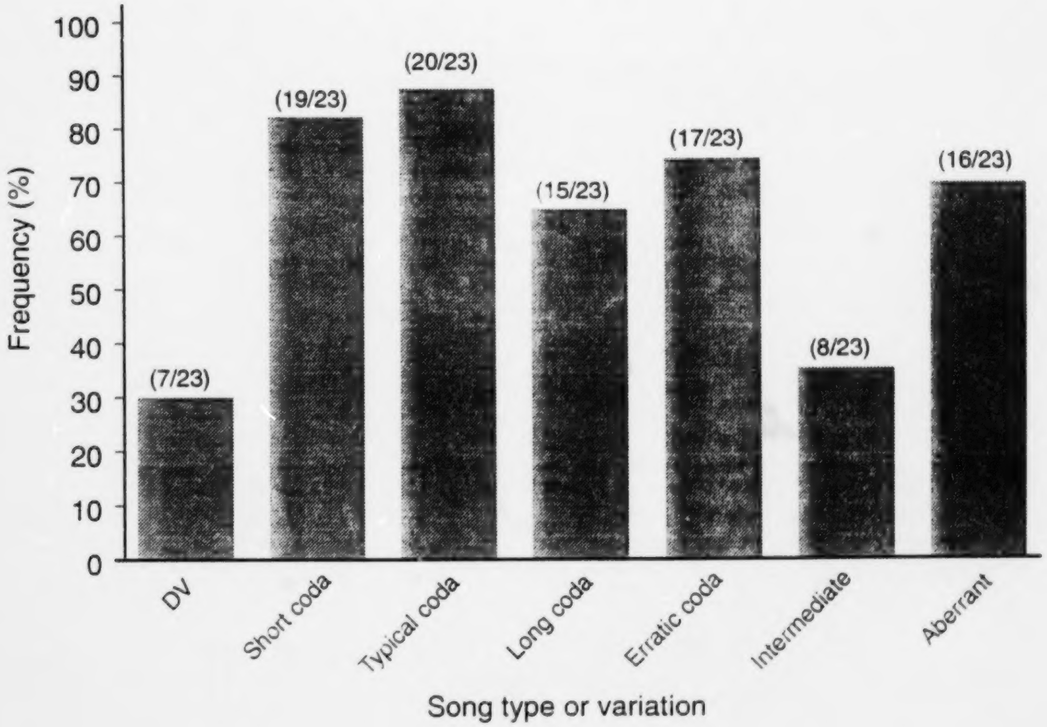

Figure 3 - 3. The percentage of males singing each of the song types or variations.

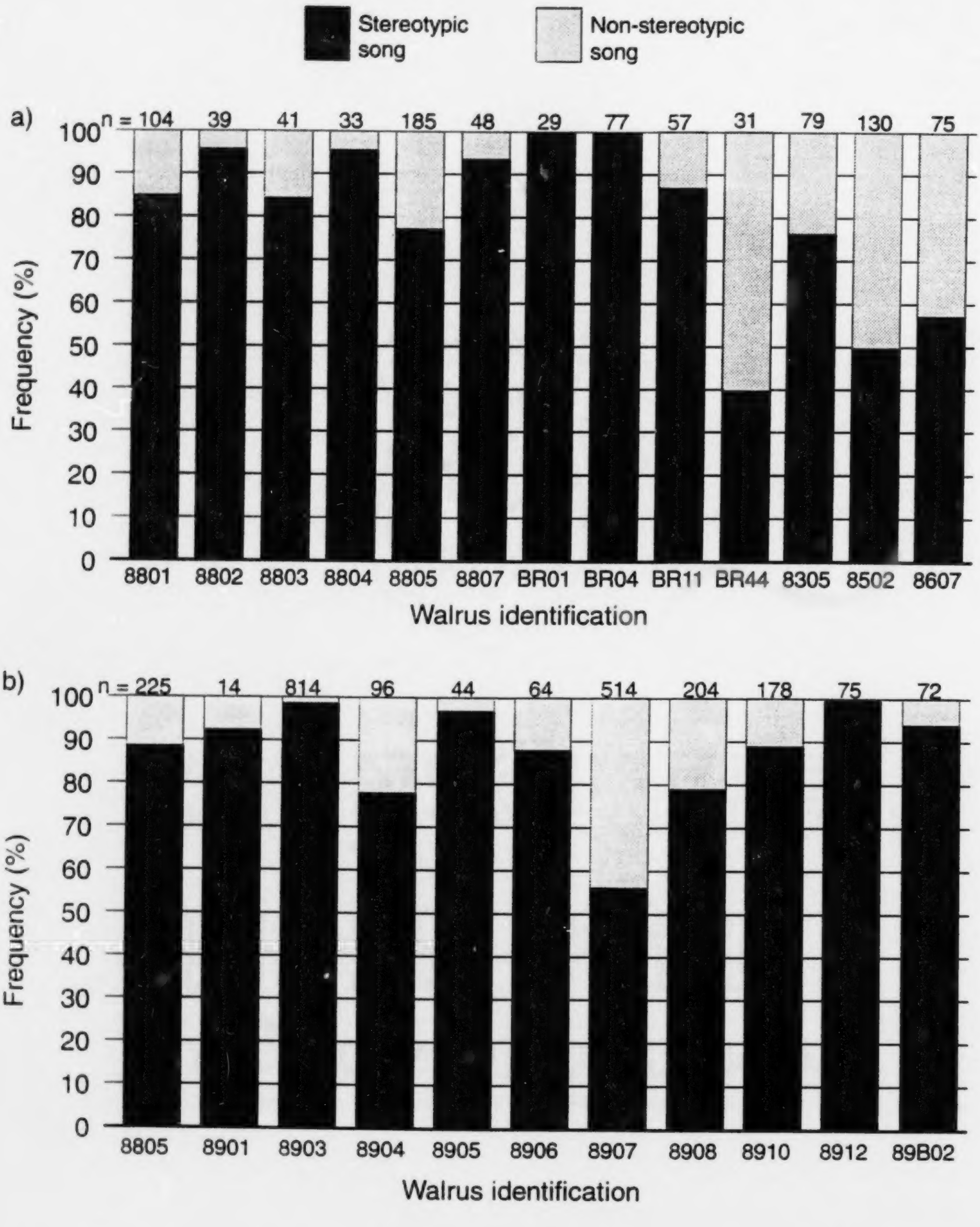

Figure 3 - 4. The occurrence of stereotypic and non-stereotypic songs emitted by males in 1983-1988 (a) and in 1989 (b). Stereotypic songs included DV songs and short, typical, and long variations of the coda song. Non-stereotypic songs included intermediate songs, aberrant songs and erratic variations of the coda song.

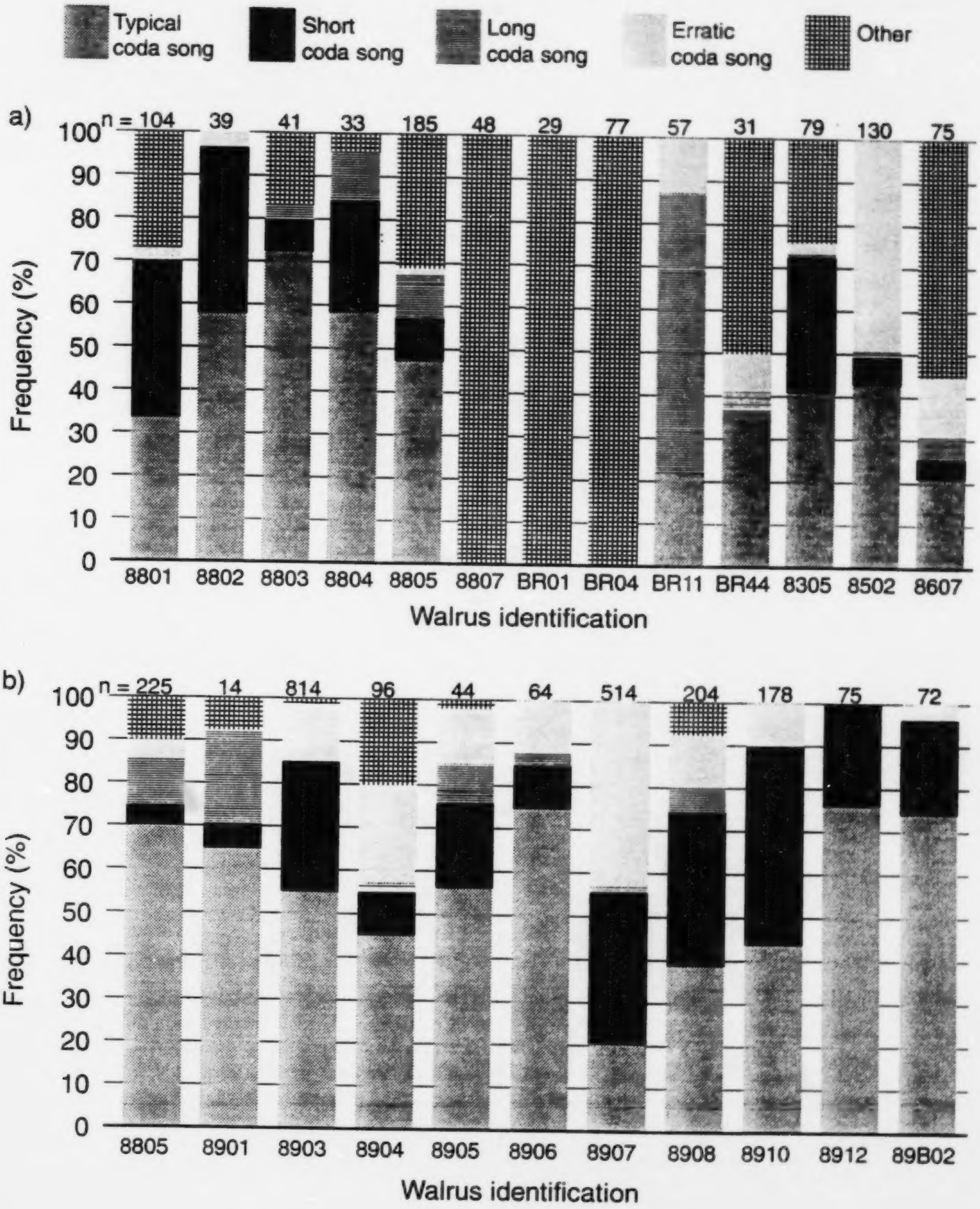

Figure 3 - 4. The occurrence of each song type or variation emitted by males in 1983-1988 (a) and in 1989 (b). Category "other" included intermediate, dv, and aberrant songs. Males 8807, BR01 and BR04 emitted dv songs at least 93% of the time. Males 8607, 8801, 8805 and 8305 emitted dv songs 27%, 13%, 7% and 1% of the time respectively.

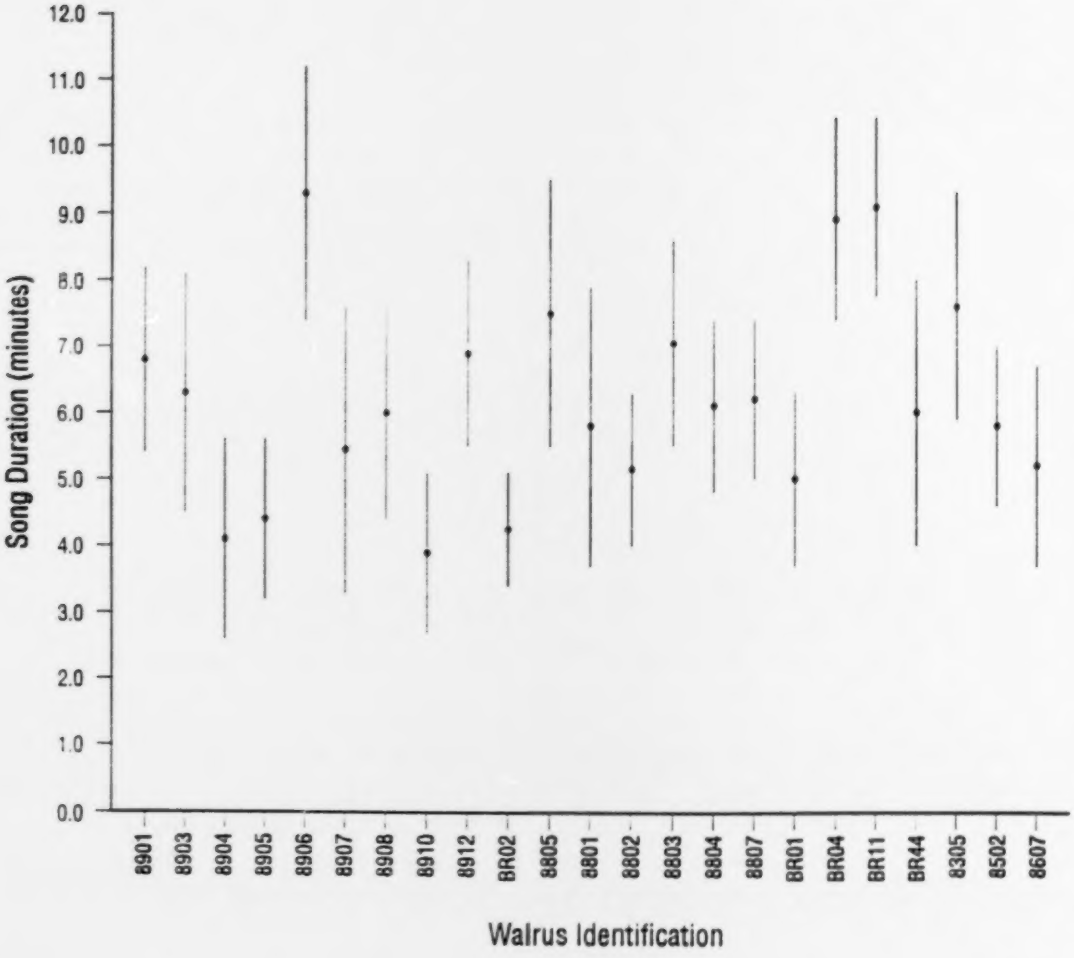

Figure 3-5 Summary of mean (SD) song durations
for each male when all song types and variations are combined.

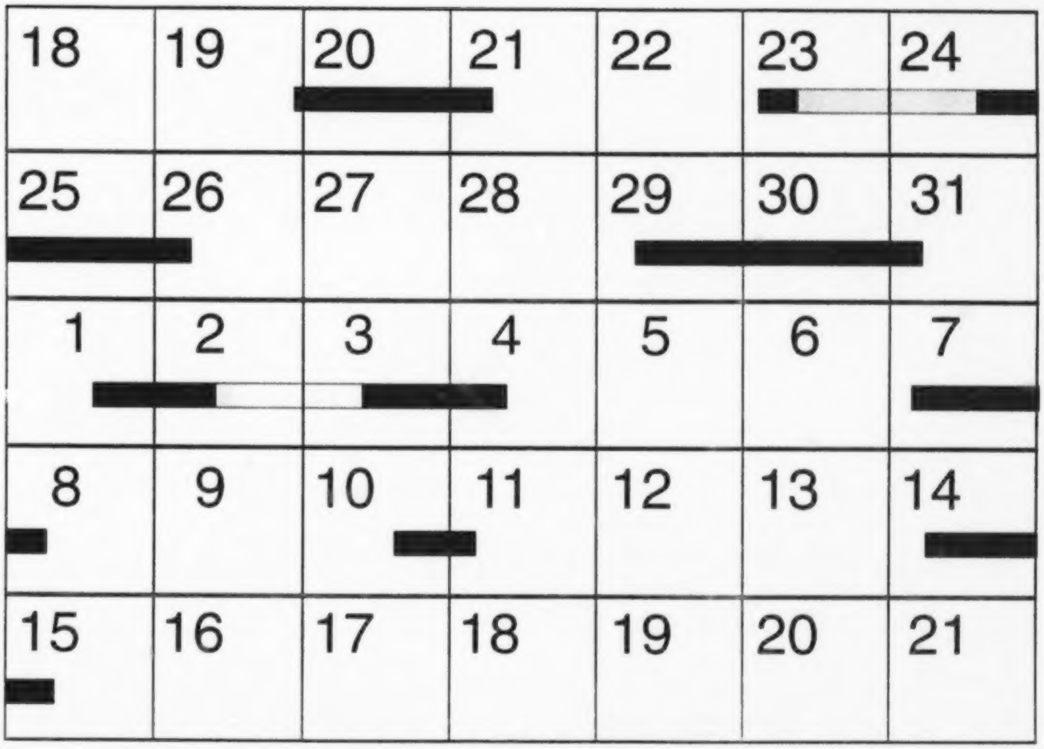

Figure 3 - 6. Singing bouts emitted by walrus 8805 during March/April, 1988. Darker shaded lines mark the time periods of continuous singing. Lighter shaded lines indicate times when observations suggest that he was singing, but cannot be confirmed.

4. VARIABILITY IN THE SURFACE CODAS OF MALE ATLANTIC WALRUSES: ARE THEY INDIVIDUALLY DISTINCTIVE?

4.1 INTRODUCTION

In the Canadian Arctic, Atlantic walruses breed and overwinter in areas of unconsolidated pack ice or polynyas (a body of open water surrounded by ice) from January to mid April (Mansfield 1958; Fay 1982). Walruses are polygynous and have a female-defense mating system where a mature male monopolizes access to a herd (or part of a herd) containing females for several days at a time (Fay 1982; Chapter 2). During his tenure, a male continuously sings a complex, stereotyped song composed of several long, patterned sequences of pulses that are punctuated with ringing bell sounds (Ray and Watkins 1975; Stirling et al. 1983, 1987; Chapter 3). The pulses are best described as knocks and taps since they sound like knuckles being rapped firmly and slowly, or tapped quickly and lightly, against a wooden surface. When males are not attending a herd or there are no females in the area they may sing alone for hours or even days at a time (Stirling et al. 1987; Chapter 3). The pattern of knocks and taps composing each long sequence, and the order in which the sequences are emitted, are surprisingly consistent among individuals and between years (Stirling et al. 1987; Chapter 3).

Two main song types have been described - the coda song and the diving vocalization song (Stirling et al. 1983, 1987). They are distinguishable from one another by the pattern of knocks and taps composing each of the long sequences, and by the presence or absence of specific vocalizations called surface codas, underwater bell-knock codas, and diving vocalizations (Ray and Watkins 1975; Stirling et al. 1983, 1987). Surface codas and underwater bell-knock codas are short, distinctive series of intense knocks that either begin or end a knocking and tapping sequence. When a walrus sings a coda song many of the sequences emitted at the surface end with a surface coda while certain underwater sequences end with a bell-knock coda. When a walrus sings a diving vocalization song no surface codas or bell-knock codas are given, but a diving vocalization is emitted just after he dives and leads into the first long underwater sequence (Stirling et al. 1987).

The surface codas, underwater bell-knock codas, and diving vocalizations produced by an individual male sound surprisingly consistent and distinctive to the human ear (Ray and Watkins 1975; Stirling et al. 1983). Stirling et al. (1987) determined that the total duration, the number of pulses, and the mean pulse repetition rate of each of these vocalizations differed significantly among males in two years. On the basis of limited data, they suggested that all three types of vocalizations were individually specific.

In this paper I assess how male Atlantic walruses vary the physical structure of their surface codas relative to recording date, social context, and song type. I then assess whether there is sufficient individual variation in surface codas to enable recognition based on them.

4.2 MATERIALS AND METHODS

4.2.1 Study area and recording techniques

An estimated 25 to 65 (Chapter 5) Atlantic walruses overwinter and breed at a recurring polynya which forms north of Cape Collins on Dundas Island (76° 09' N, 94° 52' W) in the central Canadian High Arctic (Kiliaan and Stirling 1978; Stirling et al. 1981, Chapter 5; Figure 4-1). Ice conditions in the area have been described in (Chapter 2). Observations and recordings were obtained from a hut located on a 80 m cliff overlooking the polynya. All underwater recordings were made using a Uher 4200 Report Monitor tape recorder and an International Transducer Corporation 6050C hydrophone. The effective frequency response of the recording system was either 25 - 12,000 Hz or 20 - 16,000 Hz depending on tape speed. For long recording sessions or those made for investigating daily trends a tape speed of 4.7 cm/s was used; if better quality was required the speed was increased to 9.5 cm/s. The hydrophone was either submerged through a hole in the ice or suspended over the ice shelf to a depth of 3 m along the southern edge of the polynya near the base of the cliff. Vocalizations were analysed on a Multigon Uniscan II and Kay Elemetric 7800 Sonagraph with a 150 Hz analysing filter band.

4.2.2 Description and measurement of surface codas

Surface codas are one of the major distinguishing features of the coda song (Stirling et al. 1983, 1987; Chapter 2). They are emitted while the walrus's head is submerged underwater between breaths. Most commonly 2 or 3 surface codas are given in each coda song, but the number may vary from 1 to 10. Surface codas are a short series of loud, patterned knocks which terminate a longer, and slower, sequence of knocks and taps emitted during the surface portion of the coda song (Ray and Watkins 1975; Stirling et al. 1983, 1987). Figure 4-2 illustrates the sequences of knocks and taps which characterize a typical coda song and also shows where in the song surface codas are emitted.

The following 7 variables were measured or derived for each surface coda (SC): duration of the less intense pulses at the beginning of the SC (DUR1); duration of the intense pulses at the end of the SC (DUR2); total duration (TOTDUR); an estimate of the mean interpulse interval of the beginning pulses (PRDUR1); an estimate of the mean interpulse interval of the intense pulses at the end of the SC (PRDUR2); number of intense pulses at the end of the SC (INTPUL); and total number of pulses (PULSES) in the SC (Figure 4-3). In most SCs the interpulse interval is relatively long and consistent at the beginning, and then decreases by 20 - 30% during the last part of the coda. The point where this decrease occurs is visually distinct (Figure 4-3). Total duration was measured from the start of the first pulse to the start of the last. DUR1 was measured from the start of the first pulse to the start of the pulse preceding the drop in the interpulse interval; DUR2 was estimated as (TOTDUR - DUR1). Estimates of interpulse interval for the beginning and end pulses were calculated as (DUR1 or DUR2 / number of interpulse intervals present in each component of the SC respectively).

4.2.3 Data collection and observational techniques

Underwater breeding vocalizations of walruses at the Dundas Island polynya have been recorded from 1981 through 1990 (Stirling et al. 1983, 1987, this study). Before 1987, field seasons ran from late March or early April into May. Beginning in 1987, field work started in early February. Exact field dates are given in Table 2-1. The analyses presented here are based on recordings of 1 identifiable male made in 1983, 1984 and 1987, 7 males in 1988, and 11 males in 1989. One male, 8805, was recorded in both 1988 and 1989 so information is available for 18 identified males. Table 4-1 summarizes the number of recording days, the number of recording sessions, and the hours of tape analyzed for each male.

The polynya was monitored both visually and acoustically; recordings were made whenever a singing male moved into the study area. Priority was given to recording from identifiable males if there was a choice. When possible, each walrus was recorded continuously for 2.5 hours (which in most cases meant recording at least 25 songs). If the singing male remained in the study area for longer than that, additional 1.5 hour recording sessions were taped 2 - 3 hours apart, or whenever there was a change in social activities. From 1987 to 1989, these focal recordings were supplemented with briefer recordings designed primarily to document seasonal changes in vocal activity, but they were also used to follow the singing behavior of a focal male over a long period of time. These samples were 30 min long and were taped every 3 hours on a 24 hour basis for approximately 15 days at the beginning, middle and end of the field season. Before 1987, the recordings were 20 min long and made every two hours. The sampling period was extended to 30 min to ensure that if a focal male was singing, a greater number of his songs would be recorded (at least 4).

Most male walruses were identified using drawings of tusk characteristics and scar patterns on the neck, shoulders and back. In addition to these natural marks, nine males were immobilized and branded with two-digit, 12.5 cm high, number on their hip and shoulder (Stirling and Sjare 1988). Walruses were aged and sexed using the following morphological criteria: relative size of the snout and tusks; muscular development of the upper neck and shoulders; and presence and development of tubercles (Fay 1982).

A total of 1433 SCs were selected for detailed analyses from all available recordings. In some cases, only one brief recording (i.e., <1.5 hr long) was obtained from a male, so it was necessary to include all his SCs for analysis. When a male was recorded only once, but for several hours, a block of 10 - 20 SCs was selected from the beginning, middle, and end of the vocal bout. If a male was recorded several times during the season, SCs from the beginning, middle and end of vocal bouts taped early in the season, mid season, and at the end of the season were selected for analysis. For males recorded for long periods, or recorded on more than one day, it was possible to determine how the physical structure of SCs varied with date and duration of a vocal bout.

The social contexts in which males were recorded varied considerably. The most common contexts were: singing alone with no other males visible within 100 m; singing in the presence of a silent male that remained within 50 m; and singing in the presence of females and calves. During most recordings, it was possible to hear one or more additional males singing at some distance from the focal walrus. If only a small portion of the loudest part of a background song could be heard, then the background vocalizations were considered "faint". If recognizable portions of entire song sequences could be followed easily, then the vocalizations were considered "moderately loud". When the background vocalizations were almost indistinguishable from those of the focal walrus, they were considered "loud". By sub-sampling data for males recorded in different social contexts, it was possible to evaluate how the physical structure of their SCs varied contextually.

Most males in this study sang short, typical, long and erratic variations of the coda song (Figure 3-2 in Chapter 3). Each SC analysed was noted as having come from one of the four variations, thus the relationship of song variation to SC structure was determined. Because males can give up to 10 SCs/coda song, it was possible to evaluate how SCs at the beginning of the surface portion of the song differed from those at the end.

4.2.4 Statistical analyses and data presentation

Mann Whitney U tests (MWU), Kruskal-Wallis (KW) analyses of variance, and Tukey multiple comparisons (SAS 1988; Zar 1974) were used to test whether the physical structure of SCs varied with: recording date; presence of females or a silent young male; intensity of background vocalizations; song variation; duration of the singing bout; and order of emission. KW analyses and Tukey multiple comparisons were also used to assess individual differences in SCs. For all univariate comparisons, only 6 of the 7 variables were used; INTPUL was not included because it was correlated with DUR2 and did not contribute any new information. For walruses with two SCs, G-tests (SAS 1985; Zar 1974) were used to determine if the proportion of each varied with recording date, social context, song variation, or duration of singing bout. An alpha level of 0.05 was used. Summarizing the results of statistical analyses was difficult, for several reasons. Variables often changed simultaneously in relation to different factors, and often did so in different directions. Describing how TOTDUR varied relative to different factors was the most parsimonious way of summarizing the results in the text, since changes in the other variables usually led to an overall increase or decrease in the duration of the SC. Data on each of the variables that varied significantly in relation to the different factors are presented in Appendices 1 to 6. Some males emitted two different SC types (denoted as

SC1 and SC2) and were recorded on different days. Often only one of the SCs varied significantly in response to a particular factor, or sometimes SC1 varied in one direction and SC2 in the opposite. In other situations the physical structure of one or both of the SC types varied significantly in different directions depending on recording date. Differences such as these are referred to as "inconsistent" in the text, and are listed in the appendices.

A nearest-neighbour (non-parametric) discriminant analysis was used to determine if SCs are unique to an individual (Hand 1981; SAS 1985). In this procedure observations are classified into groups (in this case, individual walruses) on the basis of several numeric classification variables (the variables measured for each SC). In both years, 6 classification variables were used in the model; INTPUL was included in 1988 and DUR1 in 1989. The best discriminant analysis model for each year was determined by examining the results of the univariate comparisons and by completing some experimental runs in which different combinations of classification variables were used. If fewer than 40 SCs were sampled for a male, then all were included in the analyses (provided the quality was good enough for reliable measurements). If sample sizes were larger, then 5 to 10% of extremely long and short SCs were excluded from the data base before a random sample of 40 to 50 SCs was taken. Half of the data set for each identified walrus was used to calculate the discriminant functions (calculation portion of run) and the remaining half, or "test" data set, was used for classification (discrimination portion of the run). An observation was placed into the group containing the highest proportion of nearest neighbors (SAS 1988). Because males that emitted two SC types were treated as if they were two individuals, the 1988 analysis was based on 8 SCs and the 1989 on 15. Male 8301, who was recorded in 1983, 1984 and 1987 was not included in these two analyses.

A sample reuse discriminant analysis technique (Gray and Schucany 1972; Mosteller and Tukey 1977) was used to quantify how well an unknown male can be distinguished from several previously identified walruses. In this procedure, the classification probabilities are estimated by first determining the best discriminant function for all observations except one, and then the derived discriminant function is used to classify the unused observation. The sample reuse technique can also be applied to an arbitrary subset of the data. In this case, the SCs of one male were withheld from the data set used in the calculation of the discriminant function and then added to the "test" data set to be classified by that function during the discrimination portion of the run. The "test" SCs simulate the vocalizations of an unknown walrus and will end up being classified to one or more of the previously recorded, or "assignable" walruses with a similar SC. Each of the walruses recorded in 1988 and 1989 was treated in this manner. Male 8301 was also used as an unknown "test" walrus for these analyses. If the discriminant function classifies a large percentage of the "test" SCs as a particular "assignable" walrus, then there is insufficient variation between the individuals to allow correct identification.

This modified discriminant analysis technique was also used to examine whether or not the SCs of an identified male recorded on different days, different years, and in different social contexts, varied enough to cause misclassification. To assess the effect of recording date, the discriminant function was calculated using SCs emitted by an identified male on a particular day or year, while the "test" data included SCs from another day or year. A similar procedure was followed for assessing the influence of social context. The discriminant function was derived using SCs that were emitted by an identified male when he was singing alone with only faint background vocalizations. The "test" data sets included SCs emitted when he was singing alone with loud background vocalizations and when he was singing in the presence of females and calves. A significant drop in the percentage of correctly classified "test" SCs would indicate that structural variations due to recording date and social conditions are sufficient enough to cause a walrus to be misidentified.

4.3 RESULTS

4.3.1 Factors affecting the occurrence of more than one type of surface coda

Coda songs were recorded from 18 males; 11 of them produced one surface coda (SC) and 7 produced two distinct types denoted as SC1 and SC2 (Table 4-1). The SC1s and SC2s of a given male were distinguished from one another by differences in the temporal patterning of the pulses and noticeable differences in their TOTDUR. These differences were apparent in sonagrams (Figure 4-4) and could also be detected by ear. In most instances, the two SC types produced by the 7 males differed significantly from each other on all 6 variables (KW test, $p<0.05$; MWU test, $p<0.05$; Tables 4-2 and 4-

3). The proportion of SC1s and SC2s emitted by an individual male ranged from about 0.5, as in the case of 8908, to showing a strong bias for one over the other (e.g., 8904; Table 4-1). In 5 of 7 males the longer SC was more common.

In 1989, two young males estimated at 6-9 years of age, were each recorded once; one walrus emitted 3 different SCs and sang an erratic variation of the coda song, the other had a single, but inconsistent SC, and also sang erratically at times. Sub-adult males recorded in the earlier years of this study also showed similarly inconsistent singing behavior (Stirling unpublished data 1981-1986). Due to the high degree of variability, these younger walruses were not included in any of the analyses presented here.

The proportions of SC1s and SC2s given by a male varied relative to: recording date; presence of females and calves in the area; intensity of background vocalizations; which variation of the coda song a male was singing at the time; order in which the SCs were given; and whether or not the SCs were emitted at the beginning, middle, or end of a vocal bout. Although small sample sizes and lack of data for some walruses hampered analyses (8904 was not included for this reason), order of emission and recording date emerged as the two most important factors determining which SC type a male emits. Four of 6 males varied the proportion of SC1s and SC2s with order; 3 walruses emitted their longer or more common SC early in the surface portion of their song (usually first or second). Male 8906 was a noticeable exception, as he emitted his shorter, less common SC first (Tables 4-1 and 4-4).

The proportion of SC1s and SC2s given varied with recording date in 2 of 4 males. Male 8903 was recorded alone on 13 February, 21 March and 15 April; he emitted a larger proportion of his longer, more common surface coda (SC2) towards the end of the season. He gave no SC1s during the April recording session (G-test, df=2, p=0.03). Male 8805 was the only walrus that sang two SC types and was recorded in more than one year. In 1988 he sang on 19 March and on 15 April; a greater proportion of his longer, more common codas (SC1) were recorded during March (G-test, df=1, p=0.001). In 1989 he sang on 27 March, 4 April and on 7 April, but this time his SC1s were more common in April (G-test, df=2, p=0.07). This male also varied the proportion of SC1s and SC2s between years. In 1988, 86% of his codas were SC1s, in 1989 the figure dropped to 53% (G-test, df=1, n=177 and 144, p<0.0001).

In 2 of 5 males the proportion of SC1s and SC2s varied during singing bouts that were longer than 1.5 hours. Male 8908 emitted the greatest proportion of his long coda (SC1) towards the end of the bout, while male 8805 (in 1988) emitted the greatest proportion of his longest and most common coda (SC1) near the beginning. The occurrence of loud background vocalizations and the coda song variation the male was singing at the time of the recording appeared to be less important than the previously mentioned factors. Too few data were available to assess whether the presence of females and calves influenced which SC type was emitted.

4.3.2 Structural variation in surface codas

Regardless of whether a male produced one or two SC types, all individuals varied the physical structure of these vocalizations to some degree in relation to recording date, social context, and coda song variation. Descriptive data and test statistics showing the physical structure of SCs in relation to each factor are in Appendices 1 to 6 and summarized in Table 4-5. A comparison of the mean number of parameters altered per SC indicates that the most important factors affecting structural variability of SCs were the presence of females and calves in the area, recording date, and the occurrence of loud background vocalizations. The variables TOTDUR and DUR1 differed most often, while DUR2 and PRDUR2 differed least often (Table 4-5).

All 5 males recorded while singing alone and in the presence of females and calves, or in the presence of a nearby silent male, varied at least one of their SCs (Appendix 1; Table 4-5). Males with only one SC, 8907 and 8910, emitted their longest SCs when singing alone. The situation was more complex for those males with two SC types. Male 8908 produced longer SC1s when alone than when a silent male was present; his SC2s were not significantly longer when singing alone. Male 8903 emitted his shortest SC1s and SC2s when alone; and male 8906 showed no systematic trends.

Eleven of 18 males were recorded when the background vocalizations varied from faint to loud. Eight of 11 males altered at least one of their SCs relative to changes in the intensity of background vocalizations (Appendix 2; Table 4-5). Six emitted their shortest SCs when there was moderately loud, or loud background vocalizations, compared to when there was only faint background vocalizations. Two males, 8906 and 8910, showed the opposite trend. Males that emitted two SC types or were recorded on different days or years did not show a consistent pattern (males 8805, 8903, 8906, and 8908).

All 3 males that sang alone and in similar social contexts showed significant differences in their SCs across recording dates (Appendix 3; Table 4-5). Male 8903 emitted his longest SCs early in the season. Both of his SC types varied in the same direction, but in the case of the SC2s, there was no indication that they gradually shortened over the 2-month period. Males 8805 and 8907 produced their longest SCs later in the season, opposite to the trend shown by male 8903. The SC1s of male 8805 recorded in 1989 were insignificantly longer at the end of the season (not shown in Appendix 3). SC2s produced by this male became progressively longer over the 9-day period.

Although males appear to show considerable fidelity to the Dundas Island polynya (Chapter 5), only two (8301 and 8805) were recorded in more than one year. Male 8301 in 1983, 1984, and 1987, and male 8805 in 1988 and 1989. Between-year comparisons indicated that there were major structural changes in the SCs of 8301 and minor changes in the SC2s of 8805 (Table 4-2). The SCs emitted by 8301 in 1987 were longer than in either of the previous years; all variables except PULSES varied significantly (KW test, $p=0.0001$; Tukey test, $p<0.05$; for all comparisons). Surface codas emitted in 1983 and 1984 were similar except that PULSES was higher in 1983 (KW test, $p=0.04$; Tukey test, $p<0.05$). Male 8805 did not vary the structure of his SC1s between years, but his SC2s were longer in 1988 than in 1989; two variables varied significantly, PULSES (MWU test, $p=0.001$) and DUR1 (MWU test, $p=0.03$).

The physical structure of one or both SC types varied in relation to their position in the singing bout in 14 of 18 males (Appendix 4; Table 4-5). Seven males (8801, 8802, 8804, BR11, BR44, 8907 and 8912) emitted their shortest SCs at the end of the bout, 2 males (8901 and 8910) emitted their longest SCs at the end, and 5 males (8805, 8903, 8904, 8906 and 8908) showed no systematic trends. In long singing bouts, most significant comparisons occurred only between the longest and shortest SCs and there was little evidence to suggest that SCs lengthened or shortened throughout the bout (for possible exceptions see 8907 and 8805 (SC2) on 20/03/88; Appendix 4).

The physical structure of one or both SC types varied with order of emission in 5 of 18 males; 2 other males showed a tendency to vary theirs (Appendix 5; Table 4-5).

Males BR11, BR02 and BR44 sang one SC type, were recorded only once, and all emitted their longest SCs towards the end of the surface portion of the coda song. Results for 8906 and 8805 showed no systematic trends. The 2 males that showed only a tendency to alter their SCs in response to order, 8912 and 8907, both emitted their longest SCs second (later in the surface portion of the song). There was no indication that PRDUR2 and DUR2 varied less than the other variables (Table 4-5).

Although mature males in the Dundas polynya area emitted coda songs that were surprisingly consistent between and among individuals, there was some variability (Chapter 3). Most males emitted a typical, short, long, and an erratic variation of the coda song. Three out of 15 males varied their SCs depending on which coda song variation was being sung; however, there were no systematic trends among the males (Appendix 6; Table 4-5). Each male varied only 1 of the 6 variables.

4.3.3 Individual variation in surface codas

The physical structure of SCs varied in response to a number of factors, but some consistent individual differences were still apparent. Analyses of variance on the 1988 and 1989 data sets showed that all 6 variables differed significantly across individuals (KW test, $df=7$, $p<0.0001$ for all analyses). Multiple-pairwise comparisons for the 1988 data set showed that between 79 and 93% of the 28 contrasts for each variable were significant (Tukey test, $p<0.05$ for all comparisons). Figures 4-5 and 4-6 summarize the mean and 95% confidence interval for the two most discriminating variables and also provide visual evidence of the individual variation in SCs.

In addition to using univariate statistics to assess individual variation, a nearest neighbor, multivariate, discriminant analysis technique was also used. Table 4-6 summarizes the percentages of SCs classified into the correct walrus identification group in 1988 and 1989 using the entire data set for each of the years and 6 classification variables. The technique displayed good discriminating power for both data sets; 87% of the SCs were correctly classified in 1988 and 88% in 1989. Misclassification rates for individual walruses ranged from 0 to 31% in 1988 and 0 to 33% in 1989.

All males included in the 1988 and 1989 analyses were in view while they sang and were positively identified. To test how successfully the discriminant functions could distinguish between SCs emitted by an unknown, or "test" walrus, and those of a previously recorded, or "assignable" walrus, a series of tests were run using a nearest-neighbor discriminant analysis technique with sample reuse. Table 4-7 lists which of the "assignable" walruses had the largest observed percentage of "test" SCs attributed to him in each run and compares it to the expected percentage if the surface codas had actually been emitted by the "assigned" walrus. The expected percentages were generated by discriminant analyses done when each "test" walrus was dropped from the data set. Nine replacement runs were completed on the 1988 data set. Observed and expected percentages differed by more than 30% in 3 cases, 15 - 30% in 4 cases, and <15% in 2 cases. Fifteen runs were completed on the 1989 data set. Observed and expected percentages differed by more than 30% in 7 cases, 15 - 30% in 4 cases, and <15% in 4 cases. The replacement runs where observed and expected percentages differed by more than 30% provide some support for the hypothesis that the codas of unknown males can be distinguished from previously recorded males.

The discriminant analysis results presented in Tables 4-6 and 4-7 were based on SCs randomly sampled from males singing on different days and in as many different social contexts as possible. This helped to maximize variation in the physical structure of SCs, and presumably improved the chances of correct classification. To determine whether recording date or social context influenced the structure of SCs enough to cause incorrect identification, another series of sample reuse discriminant analyses was run. Table 4-8 (also see Appendices 1 to 3) presents results from 10 tests when the SCs used to calculate the discriminant function and the SCs used as test data for the discrimination portion of the run were sampled from different days or different social contexts. The percentage of correctly classified SCs remained unchanged in 4 cases, decreased by 12% in two cases, decreased by 32 - 76% in 3 cases, and increased by 33% in one case. For replacement runs in which the percentage of correctly classified SCs changed by more than 30%, it appears that recording date, social context, and loud background vocalizations influenced the structure of SCs sufficiently to cause problems in walrus identification.

Only two walruses were recorded in more than one year, SCs emitted by male 8301 varied significantly between years and those of 8805 did not. A discriminant analysis with replacement data was run to determine whether SCs emitted by 8301 in 1987 were different enough from those emitted in 1983 and 1984 to be misclassified (the

1988 discriminant function was used for this analysis). A total of 87% (22/25) of the 1987 "test" SCs were misclassified indicating that the between-year differences are strong enough to prevent correct walrus identification.

4.4 DISCUSSION

4.4.1 Individual variation in surface coda vocalizations

Analysis of variance and discriminant analysis indicates that there is sufficient structural variation to identify individuals within a single breeding season. A total of 87% of SCs were correctly classified in 1988 and 88% in 1989. These classification rates are comparable to, or better than, those calculated by discriminant analysis techniques used to successfully demonstrate individual differences in other species (Hafner et al. 1979; Dahlheim 1980; Smith et al. 1982; Chapman and Weary 1990).

The results of the sample reuse discriminant analysis tests are difficult to interpret because of their qualitative nature. There were no obvious criteria that could be used to establish the degree of confidence with which one could classify a walrus as unknown or known. However, in general, the percentages of unknown "test" SCs attributed to known males were lower than would be expected had the known walruses actually emitted the SCs. Often, these differences were large: in 3/9 of the replacement runs in 1988, and 7/15 in 1989, the percentage of unknown "test" SCs attributed to one of the previously recorded walruses was at least 30% lower than would be expected had the SCs been emitted by the previously recorded walrus. Thus, it would be reasonable to assume that the "test" SCs used in each of these tests were emitted by unknown walruses. These results are preliminary, but encouraging, and represent one of the first attempts to use quantitative differences in the physical characteristics of pinniped vocalizations to identify individuals rather than simply demonstrate individual variation.

Individual variation is a prerequisite for vocal recognition, but does not establish that recognition actually occurs (Falls 1982). Walruses are probably capable of hearing at least the same differences in SCs as the human ear can (Schusterman 1981; Moore and Schusterman 1987). However, playback experiments are necessary to show that walruses can discriminate among individuals on the basis of SCs. It was not possible to conduct playback experiments in this study, but observations of the spacing behavior of singing males that were not in visual contact suggests that young adult males recognize the vocalizations of older, more dominant males, and will either leave the area or become silent when approached (Chapter 2). In addition, observations suggest that certain mature males change their spacing or singing behavior in response to the loud vocalizations of other particular individuals (Chapter 2). These observations support the idea that SCs, (and perhaps other vocalizations as well), contain information on identity and could function as individually distinctive vocalizations.

However, SCs do vary in a number of respects which, in certain situations, could make it difficult for their use as individually distinctive vocalizations. Some mature males have two SC types and juvenile and sub-adult males have been known to emit three or more highly variable SCs. Almost all males varied the physical structure of their SCs to some degree in relation to recording date, social context, and song variation. Information on the two males recorded in more than one year indicated that the physical structure of SCs may vary significantly between years.

4.4.2 Identification of males with two surface coda types

Seven of 18 mature males emitted two distinct SC types. Both univariate and multivariate analyses indicated that the types were as distinctive from each other as they were from the SCs of other individuals. The occurrence of more than one SC type complicated analyses, but did not prohibit them. In some cases the proportions of each type changed significantly with recording date and whether they were emitted near the beginning or end of the surface portion of the song. These shifts did not seriously affect identification because a relatively large number of SCs were sampled for each walrus, and sometimes the same walrus was recorded on different days. However, a problem could arise if an unseen male is recorded while he is emitting only one of his SCs, and then, several days later he is recorded emitting the other. Assigning both SCs to a single male, and then correctly determining if he had been recorded previously would be difficult. Correct identification would depend on how distinctive his SCs were, the quality and length of the recordings, the number of times he was recorded, and the number of other males in the study area. Based on available information from identified males, the chance of this scenario occurring is small; it happened once with 8903 in 1989 and not at all in 1988.

It is not known why some males emit two SC types and others do not - age or social status do not appear to be determining factors. A male that regularly alternates between two SC types is easier for a human observer to identify than a male with only one SC that closely resembles one or two other males. It would be difficult to determine how sensitive walruses are to such variability. Silent, young males follow and copy the diving and breathing pattern of mature, singing males (Chapter 2). This behavior most likely allows young males to learn and develop their songs; however, it may also play an important role in shaping the structural characteristics of the younger male's SC.

On the basis of present information, it appears that SCs cannot be used to reliably identify males younger than an estimated age of 10 years. This problem limits the use of SCs as individually distinctive vocalizations, but does not invalidate the technique. A young male can usually be distinguished from a mature male by the overall inconsistency of his song (Stirling unpublished data 1981-1989), and his SCs can then be excluded from further analyses.

4.4.3 Walrus identification and the problem of structural variations in surface codas

Sixteen of 18 males showed significant variation in the physical structure of at least one of their SCs in relation to a number of different factors. The most important of these being, the presence of females and calves nearby, recording date, and occurrence of loud background vocalizations. Of the 6 variables considered for each SC, TOTDUR and DUR1 varied the most and DUR2 and PRDUR2 the least. Some trends emerged, but sample sizes were too small to draw firm conclusions in most cases. Three of 5 males shortened their SCs when they were singing near a herd of females and calves; 6 of 8 males shortened one or both of their SCs when there were loud background vocalizations; and 2 of 3 males emitted shorter SCs early in the season. Between-year comparisons of the two males recorded in more than one year showed that SCs sung by 8301 differed significantly relative to 5 of 6 variables over 4 years, while 8805 showed only minor differences between two seasons.

Variability in the structure of SCs did not cause serious identification problems in the initial discriminant analyses because males that sang in more than one social context or on more than one day were adequately sampled. However, this was not the case when the sample reuse discriminant analyses were run to evaluate if a male could be correctly identified when he was recorded for a short period of time on two occasions several weeks apart, or in two very different social contexts. In 3 of 10 runs structural variations caused a decrease in the number of correctly classified SCs. Not enough is known about the seasonal variability of SCs to compensate for differences due to recording date. This problem limits our ability to use SCs as individually distinctive vocalizations. Variability in the structure of SCs relative to social context, particularly the presence of females and the occurrence of loud background vocalizations is not a serious problem. When a male is singing near a herd of females and calves there are usually distinctive outbursts of vocalizations emitted by satellite males as well as grunting and barking sounds emitted by the females and calves (Chapter 2 and unpublished data 1987-1989). These vocalizations can serve as cues to indicate the presence of females even though no walruses can be seen. Surface codas recorded in this situation should be considered separately, or in some cases, not used for identification. Because loud background vocalizations occur sporadically, it is often possible to record a focal male during an extended quiet period.

The importance of between-year variation in the structure of SCs cannot be assessed because only two males were recorded in more than one year and the results were inconsistent. Until more information is available, between-year variations remains one of our most serious problems limiting the reliable use of SCs as individually distinctive vocalizations on a longer term basis.

The sample reuse discriminant analyses included only those SCs that were emitted by males recorded on widely varying dates and in the most contrasting social contexts. In a typical field setting, these situations are uncommon and the chance of incorrect identification is likely to be less of a problem. In addition, only SCs have been analysed in detail; diving vocalizations and underwater bell-knock codas (and perhaps other parts of the song) may also contain information on identity (Stirling et. al. 1987). In the future, it should be possible to use these vocalizations to improve the chances of correctly identifying males.

It is important to recognize that there are two questions being asked about SCs. Can walruses potentially use SCs to recognize other walruses v.s. can researchers consider them as individually distinct vocalizations? The results of the sample reuse discriminant analyses do not invalidate the possible use of SCs for individual recognition by walruses. However, they do indicate that there are limits for the reliable use of SCs as individually distinctive vocalizations from the researcher's perspective.

4.4.4 Adaptive significance of individually distinctive vocalizations

The occurrence and function of individually distinctive whistles (i.e., signature whistles) in small cetaceans has received considerable attention in the past (Caldwell and Caldwell 1965, 1971; Tarnski 1976; Dahlheim 1980). These studies showed that some small cetaceans emit individually distinctive whistles. However, some authors (e.g., Tavolga 1983) felt that more information was needed to confirm that these whistles were being used for individual recognition and that they were not artifacts of captivity. More recent studies have shown that free-ranging bottlenose dolphins, *Tursiops truncatus*, temporarily enclosed in a net corral also emit individually distinctive whistles (Sayigh et al. 1990). Long-term data on individually identified bottlenose dolphins indicate that whistles can remain stable for at least 12 years and that they appear to be important in maintaining the social structure of the community (Sayigh et. al. 1990). There is considerably less known about vocal individuality in larger cetaceans. Watkins and Schevill (1977) suggested that sperm whale codas may be individually specific, although Weilgart and Whitehead (1988) found that they could only distinguish mature from immature males. Other species for which there is evidence of individually specific vocalizations include killer whales, *Orcinus orca* (Dahlheim 1980) and humpback whales, *Megaptera novaeangliae* (Hafner et al. 1979).

Evidence for individually distinctive vocalizations is available for several species of pinnipeds, including: northern elephant seals, *Mirounga angustirostris*, (Bartholomew and Collias 1962; Le Boeuf 1969; Shipley *et al.* 1981); California sea lions, *Zalophus californianus* (Schusterman and Dawson 1968; Schusterman 1977; Cenami et al. 1992); South American fur seals, *Arctocephalus australis* (Trillmich and Majluf 1981); Guadalupe fur seals, *A. townsendi* (Pierson 1978); South African fur seals, *A. pusillus doriferus*, and New Zealand fur seals, *A. forsteri* (Stirling and Warneke 1971). In his review of vocal recognition in birds, Falls (1982) used comparative studies to relate the distinctiveness of a bird's song or vocalization to its social organization and signalling needs. He concluded that selection has enhanced vocal individuality in species where it is advantageous. Observations on the behavior of male walruses during the breeding season at the Dundas Island polynya suggest that individual vocal recognition would be advantageous.

The breeding strategy of walruses at the Dundas Island polynya is best described as a female-defense system where only large mature males, that are at least 10-15 years of age gain access to a herd of females (Chapter 2). Most of these males have fresh wounds and numerous scars on their necks, shoulders, and upper back areas, indicating that fights to establish social status occur. However, during the study period, from approximately 10 February to 1 May, surprisingly few fights were observed, suggesting that they may take place at the start of the breeding season (mid January). Observations of male-male spatial interactions and singing behavior suggest that vocalizations provide information that facilitates the maintenance of dominance relationships (Chapters 2 and 3). Such communication would allow males to reduce the amount of energy and risk involved in aggressive interactions associated with the acquisition or defense of females. When a mature high-ranking male approaches a herd of females with an attending male, he represents a potential threat for take-over of the herd; thus, the ability of the attending male to recognize and respond appropriately to the potential challenger could be important. The occurrence of complex interactions between attending males, silent male herd members, and satellite males (Chapter 2) suggests that it may also be important for young males to be able to recognize the songs of particular dominant males and adjust their behavior to maximize their contact with females in the area while not inciting an aggressive response from the dominant males.

Breeding walruses are difficult to observe because of inclement weather, low light conditions, and variable sea-ice conditions. Given that a mature male can be identified on the basis on his SCs for at least one breeding season, these vocalizations could be used as acoustic tags to obtain more detailed information on the social organization of walruses during the breeding season, male mating strategies, and winter habitat use. In the future it may be possible to combine the use of SCs as acoustic tags with a hydrophone array system to pinpoint the locations of singers to obtain a more detailed knowledge of walrus breeding ecology.

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Table 4-1. Summary of recordings for each walrus and comments on the occurrence of surface coda variations.

Walrus identification	Number of days recorded	Number of recording sessions	Hours of tape analysed	Number of SCs measured	Number of SC variations	% Frequency of occurrence for each SC variation	General comments on TOTDUR
8801	1	1	4.70	54	one	N/A	
8802	1	1	3.05	32	one	N/A	
8803	1	3	3.50	33	two	SC1 72.7; SC2 27.3	SC2 longer
8804	1	2	2.10	36	one	N/A	
BR11	1	2	3.55	37	one	N/A	
BR44	1	1	3.15	39	one	N/A	
8805 (1988)	5	13	12.80	177	two	SC1 85.9; SC2 14.1	SC1 longer
(1989)	4	7	12.68	144	two	SC1 52.8; SC2 47.2	SC1 longer
8301 (1983)	2	2	1.88	28	one	N/A	
(1984)	3	3	3.17	45	one	N/A	
(1987)		1	4.53	49	one	N/A	
8901	1	1	1.58	40	two	SC1 77.5; SC2 22.5	SC1 longer
8903	5	9	15.03	219	two	SC1 33.3; SC2 66.7	SC2 longer
8904	2	2	3.28	70	two	SC1 92.9; SC2 7.1	SC2 longer
8905	1	1	1.15	32	one	N/A	
8906	2	2	3.20	64	two	SC1 45.3; SC2 54.7	SC2 longer
8907	4	7	9.32	114	one	N/A	
8908	2	3	6.95	76	two	SC1 52.6; SC2 47.4	SC1 longer
8910	2	3	3.57	66	one	N/A	
8912	1	1	.90	29	one	N/A	
BR02	1	1	2.05	49	one	N/A	

Table 4-2. Descriptive statistics for surface codas recorded from males in 1983, 1984, 1987 and 1988 ($\bar{x} \pm SD$).

Walrus identification	Pulses	TOTDUR (ms)*	DUR1 (ms)	PRDUR1 (ms)	DUR2 (ms)	PRDUR2 (ms)
8801	11.50 ± 1.01*	1479 ± 136	990 ± 130	143 ± 13	489 ± 59	112 ± 6
8802	15.00 ± 1.20	1704 ± 127	1084 ± 96	110 ± 7	620 ± 61	109 ± 8
8803 (SC1)	8.04 ± 0.20	1112 ± 21	649 ± 19	216 ± 6	463 ± 10	116 ± 3
(SC2)	9.22 ± 0.67	1373 ± 48	990 ± 44	163 ± 7	383 ± 1	123 ± 4
8804	14.80 ± 0.91	1867 ± 16	1159 ± 108	143 ± 10	708 ± 70	115 ± 8
BR11	15.10 ± 0.87	2107 ± 125	1309 ± 107	152 ± 6	798 ± 6	124 ± 2
BR44	11.23 ± 1.01	1596 ± 106	989 ± 80	159 ± 12	607 ± 89	126 ± 11
8805 (SC1) 1988	15.46 ± 1.01	1901 ± 117	1105 ± 95**	133 ± 99	796 ± 70	110 ± 7
(SC2) 1988	13.43 ± 0.98	1689 ± 125	1085 ± 111**	134 ± 9	603 ± 63	105 ± 4
8805 (SC1) 1989	15.44 ± 1.13	1928 ± 142	1140 ± 113	129 ± 16	778 ± 52	110 ± 4
(SC2) 1989	12.76 ± 0.89	1640 ± 98	1081 ± 70	136 ± 9	558 ± 76	105 ± 5
8301 (1983)	15.18 ± 1.06	1890 ± 109	1219 ± 99	137 ± 4	671 ± 68	107 ± 3
(1984)	14.42 ± 1.20	1802 ± 148	1163 ± 146	140 ± 63	640 ± 63	106 ± 4
(1987)	14.74 ± 1.41	2080 ± 190	1386 ± 165	152 ± 5	694 ± 78	117 ± 4

* Milliseconds

** All comparisons between SC1 and SC2 are significantly different except this one

Table 4-3. Descriptive statistics for surface codas recorded from males in 1989 ($\bar{x}$ ± SD).

Walrus identification	Pulses	TOTDUR (ms)*	DUR1 (ms)	PRDUR1 (ms)	DUR2 (ms)	PRDUR2 (ms)
8904 (SC1)	12.32 ± 0.77*	1586 ± 140	869 ± 136	153 ± 6	726 ± 75	122 ± 2
(SC2)	14.80 ± 0.45	2020 ± 79	1095 ± 111	153 ± 4	925 ± 78	122 ± 8
8905	12.63 ± 1.19	1669 ± 116	1071 ± 103	154 ± 5	599 ± 54	118 ± 3
8907	14.18 ± 1.13	1609 ± 176	878 ± 156	138 ± 40	731 ± 70	98 ± 5
8910	14.55 ± 1.32	1839 ± 162	1204 ± 139	127 ± 8	635 ± 79	116 ± 6
8912	13.41 ± 0.63	1608 ± 43	858 ± 34	135 ± 7	750 ± 32	109 ± 4
BR02	15.60 ± 1.18	1811 ± 77	1154 ± 68	110 ± 4	657 ± 53	112 ± 2
8901 (SC1)	13.70 ± 0.82	1589 ± 99	964 ± 86	133 ± 3	625 ± 3	108 ± 3
(SC2)	11.33 ± 0.87	1730 ± 132	1269 ± 137	136 ± 3	461 ± 87	112 ± 4
8903 (SC1)	9.94 ± 0.73	1543 ± 83	1162 ± 78	150 ± 15	382 ± 18	126 ± 8**
(SC2)	10.93 ± 1.33	1655 ± 136	1111 ± 98	156 ± 14	544 ± 73	128 ± 5**
8906 (SC1)	9.17 ± 2.07	1366 ± 199	1092 ± 166	135 ± 9	274 ± 86	112 ± 23
(SC2)	15.94 ± 1.26	2168 ± 184	1186 ± 102	145 ± 6	982 ± 128	123 ± 5
8908 (SC1)	13.38 ± 1.39	1826 ± 205	1133 ± 208	151 ± 10	693 ± 59	137 ± 10**
(SC2)	10.39 ± 1.48	1493 ± 207	939 ± 209	179 ± 19	554 ± 37	136 ± 6**

* Milliseconds; ** All comparisons between SC1 and SC2 are significantly different except these two

Table 4-4. The relationship of order to surface coda type emitted.

Walrus identification	Surface coda type	Percentages of each SC variation emitted first, second, or third during the surface portion of the coda song			G-test results
		First	Second	Third	
8906[*]	SC1 (n=29)	51.7	31.0	17.2	
	SC2 (n=35)	5.7	20.0	74.3	26.522; p=0.0001
8908	SC1 (n=40)	51.4	40.5	8.1	
	SC2 (n=36)	36.2	44.4	19.4	6.974; p=0.031
8901[**]	SC1 (n=31)	51.6	48.4	0	
	SC2 (n= 9)	44.4	11.2	44.1	15.156; p=0.0001
8805[*]	SC1 (n=76)	40.8	48.7	10.5	
(1989)	SC2 (n=68)	35.3	35.3	29.4	8.554; p=0.014

[*] For 8906 and 8805 (1989) all third, fourth and fifth codas were combined

[**] For 8901 the order categories were first and second codas combined, third and fourth combined, and fith and sixth combined

Table 4-5. Summary of the factors with significant effects on the structure of surface codas. Information taken from Appendices 1-6.

Influencing factor	Number of SCs affected	Number of significant KW or MW-U comparisons	No. variables altered for each SC mean (SD)	Percent of significant comparisons attributed to each variable					
				Pulses	TOTDUR	DUR1	PRDUR1	DUR2	PRDUR2
Recording date	6*	16/36	2.67 (1.21)	18.8 (3/16)	25.0	25.0	6.3	12.5	12.5
Presence of females and calves nearby	7	26/42	3.70 (0.95)	19.2 (5/26)	26.9	23.1	15.4	7.7	7.7
Presence of loud background vocalizations	9	23/54	2.56 (1.33)	17.4 (4/23)	17.4	30.4	21.7	4.3	8.7
Location in song-bout	20	41/120	2.05 (1.10)	22.0 (9/41)	26.8	12.2	19.5	9.8	9.8
Order	7	13/42	1.86 (1.07)	15.4 (2/13)	23.1	7.7	15.4	15.4	23.1
Coda song variation	3	3/18	—	—	—	—	—	—	—

* Some males emitted two SC types and sometimes only one of those SC would vary in response to a particular factor.

Table 4-6. Nearest-neighbor discriminant analysis based on vocalizations from all walruses and using six classification variables.

1988			1989		
Walrus identification	N	% of surface codas classified correctly	Walrus identification	N	% of surface codas classified correctly
8801	6	77	8805 (SC1)	20	78
8802	16	94	8805 (SC2)	19	100
8803	12	100	8901	15	77
8804	16	69	8903 (SC1)	33	93
8805 (SC1)	29	83	8903 (SC2)	34	97
8805 (SC2)	10	100	8904	24	100
BR11	17	94	8905	16	93
BR44	18	78	8906 (SC1)	12	85
			8906 (SC2)	14	100
			8907	33	90
			8908 (SC1)	13	93
			8908 (SC2)	18	87
			8910	27	67
			8912	15	93
			BR02	25	73

Table 4-7. Use of nearest-neighbor discriminant analyses with sample reuse to distinguish between unknown "test" walruses and previously recorded walruses in 1988 and 1989.

Identity of "Test" Walrus	% of "Test" SCs Classified to a Particular "Assignable" Walrus (=observed)	Identity of "Assigned" Walrus	% of SCs emitted by the assigned walrus that were correctly classified (=expected)	Comparison of observed and expected percentages
8801	46	8805 (SC2)	90	44% lower
8802	50	8804	69	19% lower
8803	100	BR44	83	22% higher
8804	50	BR11	94	44% lower
8805 (1988)	69	8804	75	6% lower
8805 (SC2) (1988)	60	8805	86	26% lower
BR11	100	8804	88	12% higher
BR44	57	8801	93	36% lower
8301 (1987)	65	BR11	94	29% lower
8805 (1989)	33	8901	77	44% lower
8805 (SC2) (1989)	55	8910	67	12% lower
8901	46	8805	83	37% lower
8903	79	8903 (SC2)	97	18% lower
8903 (SC2)	63	8903	93	30% lower
8904	78	8905	100	22% lower
8905	37	8904	100	43% lower
8906	62	8903	93	31% lower
8906 (SC2)	88	8904	100	12% lower
8907	97	8912	93	4% higher
8908	57	8904	100	43% lower
8908 (SC2)	80	8903 (SC2)	100	20% lower
8910	53	BR02	96	43% lower
8912	93	8805	72	21% higher
BR02	86	8910	90	4% higher

Table 4-8. Results of nearest-neighbor discriminant analyses with sample reuse to determine if the physical structure of surface codas varies enough with social context to cause misidentification. Information is taken from Appendices 1-3.

Walrus identification	Data set used for each run (calculation vs. discrimination)	Percent of SCs classified correctly in calculation run	Percent of "test" SCs classified correctly in discrimination run	Comparison of percentages - observed to exspected
Effect of recording date:				
8903(SC2)	13\02\89 vs. 21\02\89	100	88	12% lower than expected
8907	07\03\89 vs. 19\03\89	67	100	33% higher than expected
Effect of social situation:				
8903	alone vs. females present	100	100	no change
8903(SC2)	alone vs. females present	97	85	12% lower than expected
8907	alone vs. females present	96	96	no change
8910	alone vs. females present	86	10	76% lower than expected
Effect of background singing				
8904	moderately loud vs. loud	100	68	32% lower than expected
8907	none vs. moderately loud	86	89	no change
8908(SC2)	faint vs. moderately loud	100	100	no change
8910	none vs. loud	81	36	45% lower than expected

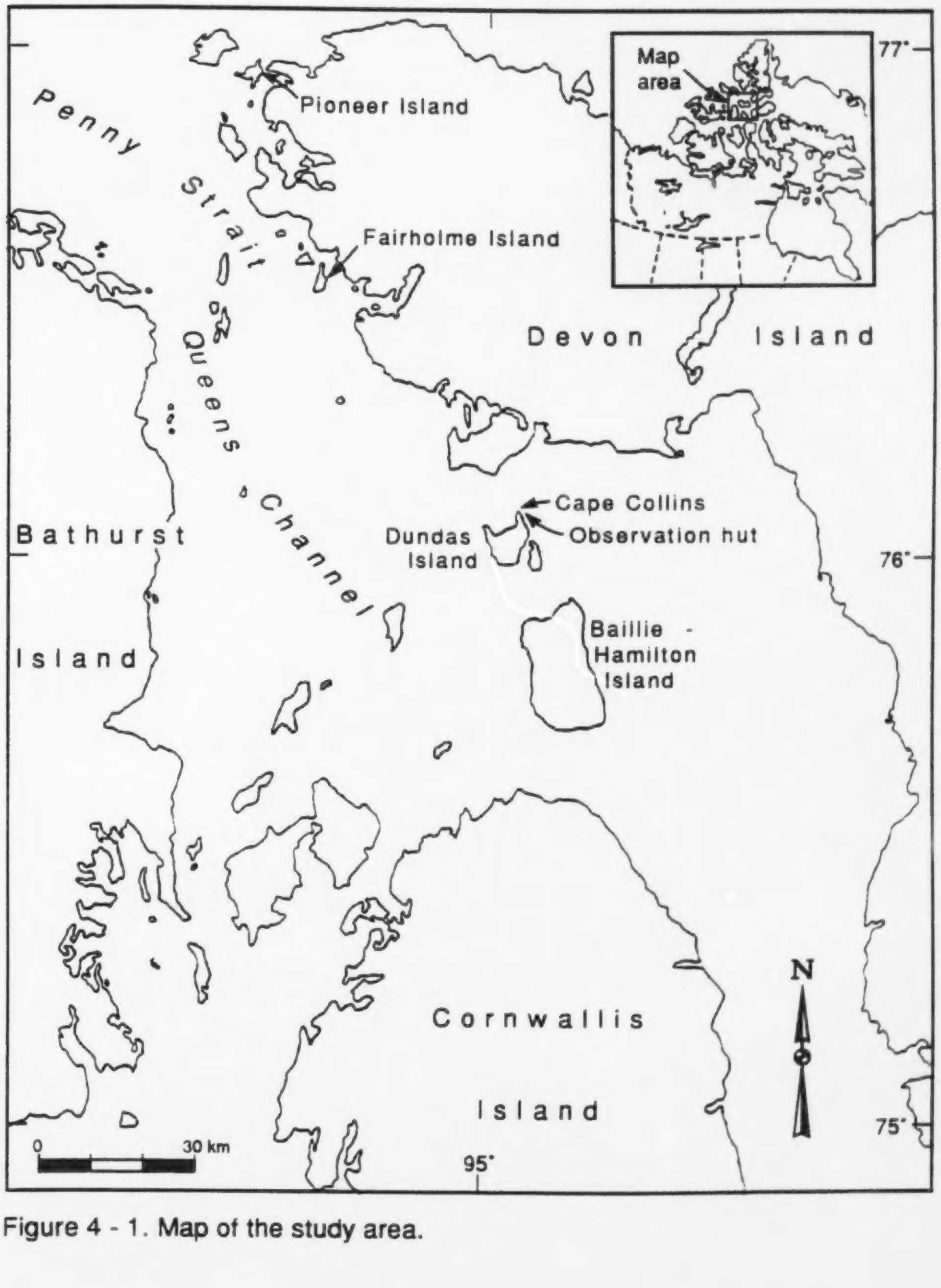

Map area
77°
Penny Strait
Pioneer Island
Fairholme Island
Queens Channel
Devon Island
Cape Collins
Observation hut
Dundas Island
Bathurst Island
76°
Baillie - Hamilton Island
N
Cornwallis Island
0
30 km
95°
75°

Figure 4 - 1. Map of the study area.

Typical Coda Song

Surface Portion	1)	k 4k	breath
	2)	k 4k -- ts -- surface coda	breath
		k 4k	breath
		k 4k -- ts -- surface coda	breath
		k 4k	breath
		k k	walrus dives
Underwater Portion	I	Long ks -- bk -- bkc	
	II	2t -- ks -- dk - bk	
	III	bk -- long, fast ts -- k - bk -- long ks -- bkc	
	IV	3t -- short ks -- series of bks -- 2k	walrus surfaces and song is repeated

Figure 4 - 2. Schematic representation of a typical coda song showing where surface codas are emitted. Summary of abbreviations used: bk, bell-knock; dk - bk, double-knock bell-knock; bkc, bell-knock coda; ks, knocking sequence; ts, tapping sequence; k, single knock which is distinctive; t, single tap which is distinctive.

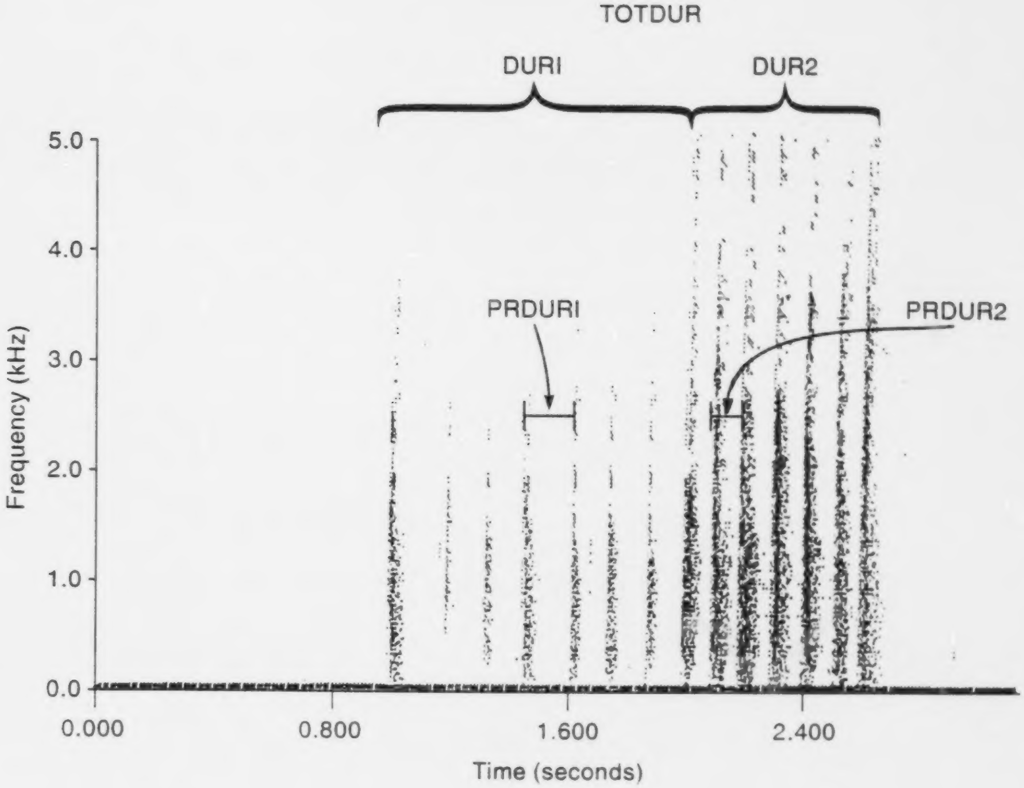


Figure 4 - 3. Spectrogram of a surface coda showing how each of the variables were measured. This surface coda has 7 intense pulses and 14 pulses in total.

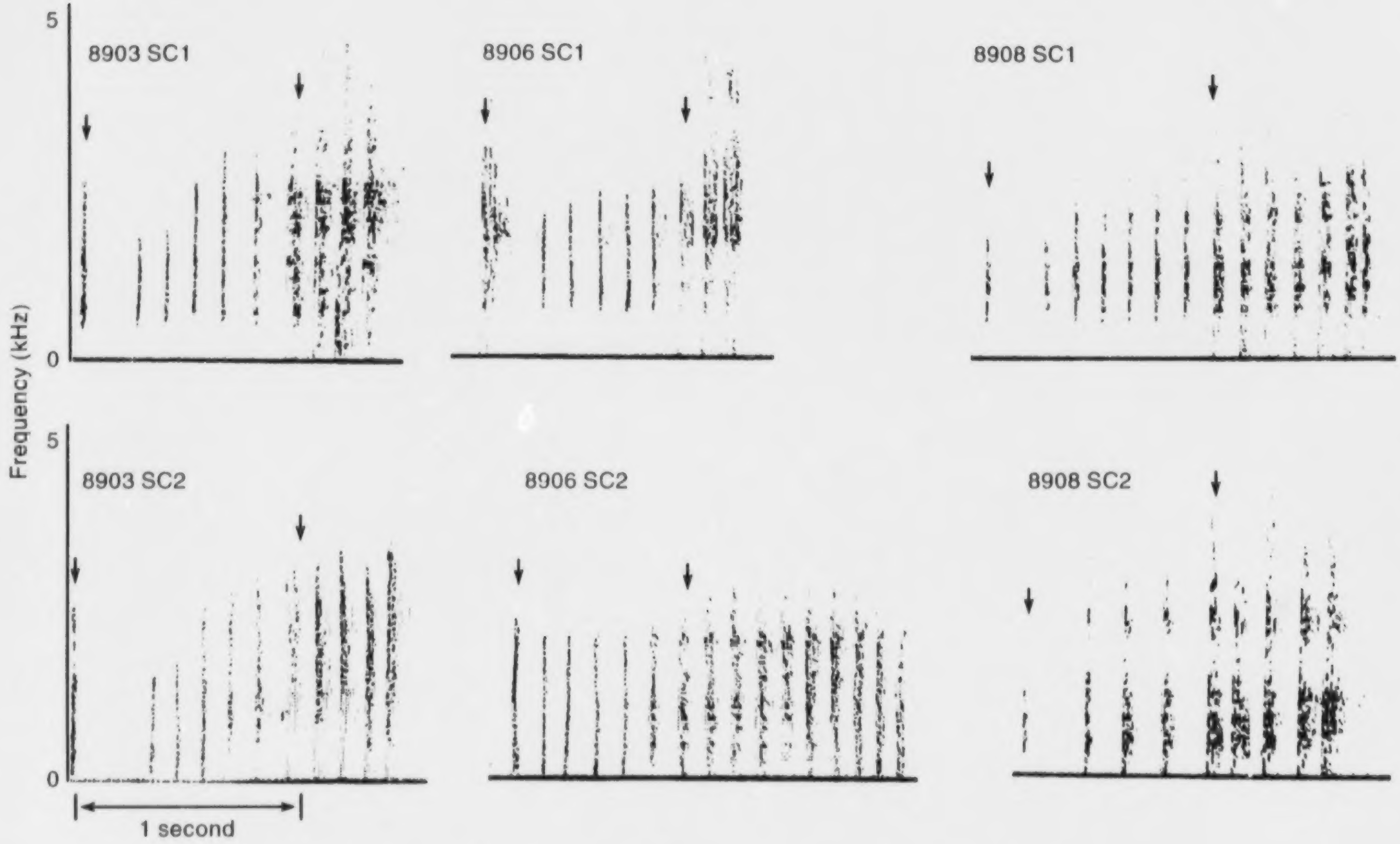
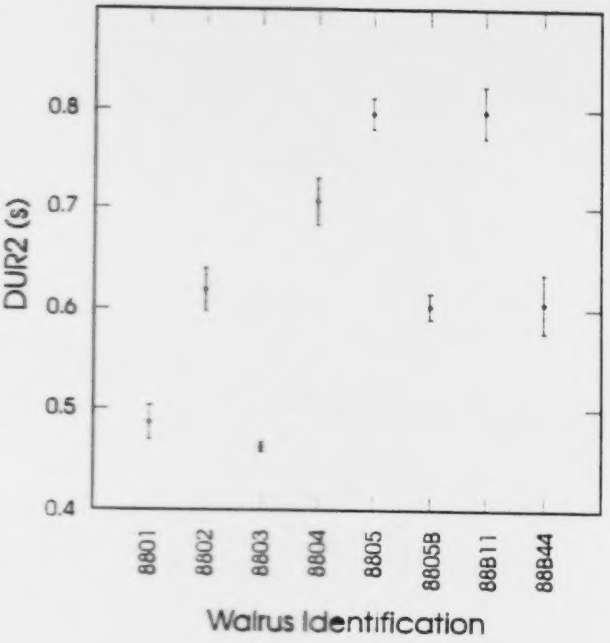


Figure 4 - 4. Spectrograms of SC1s and SC2s emitted by three males. Arrows indicate the start of the surface coda and the start of the DUR2 component. Spectograms are arranged to highlight the variability in the DUR2 component of the surface coda. Male 8906 showed the most extreme differences between his two surface codas while 8903 showed the least.



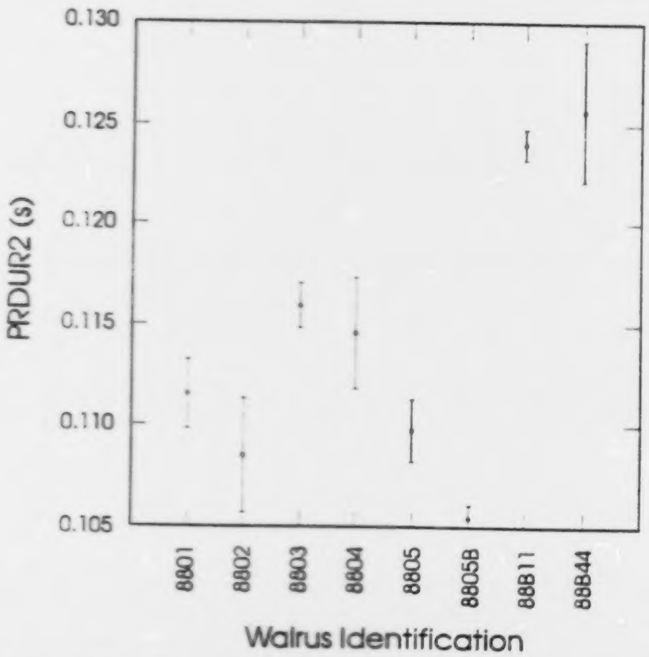


Figure 4-5a. Mean and 95% confidence interval for DUR2 and PRDUR2 measured from surface codas recorded in 1988. DUR2 and PRDUR2 are the two best discriminating parameters.

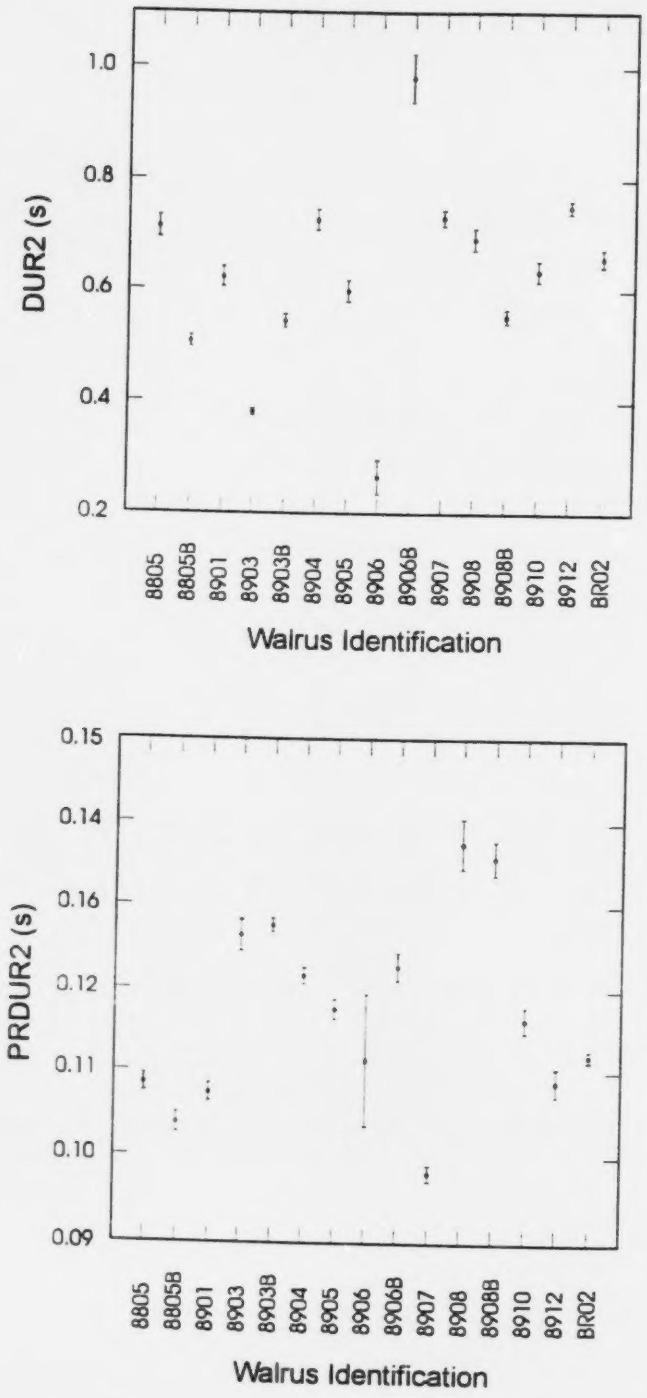


Figure 4-5b. Mean and 95% confidence interval for DUR2 and PRDUR2 measured from surface codas recorded in 1989.

5. COMMENTS ON THE DISTRIBUTION AND ABUNDANCE OF ATLANTIC WALRUSES IN THE CENTRAL CANADIAN HIGH ARCTIC DURING THE BREEDING SEASON

5.1 INTRODUCTION

In Canada, Atlantic walruses inhabit the coastal waters of northern Hudson Bay and Foxe Basin (Mansfield 1958, Loughrey 1959; Mansfield and St. Aubin 1991), the eastern coast of Baffin Island, the central High Arctic (Bissett 1968; Davis et al. 1978; Kiliaan and Stirling 1978), and the western coast of Greenland (Vibe 1950, 1956; Loughrey 1959). Approximately 10,000 walruses are thought to inhabit Canadian waters, but there are few reliable estimates of population size for specific areas, and it is unknown how many discrete stocks exist (Reeves 1978). The population of walruses in the Penny Strait region of the central High Arctic is small and is distributed near the western and northern limits of this subspecies' range. The first systematic surveys to estimate the number of walruses in this region were conducted in mid April, early June, mid July and late August of 1977 (Davis et al. 1978). Based on these surveys, it is estimated that 200 walruses overwinter in or near polynyas in the Penny Strait region: 25 in the Dundas Island polynya and 175 in coastal areas along the Grinnell Peninsula (Figure 5-1). No behavioral observations were reported from their surveys.

The abundance, distribution, movements, and habitat requirements of walruses during the winter breeding season are generally unknown. Most walruses overwinter in inaccessible regions of drifting pack-ice; smaller more localized populations overwinter in polynyas (Mansfield 1958; Kiliaan and Stirling 1978; Stirling et al. 1981; Fay 1982). The two habitats differ from each other in scale and in the relative stability of the sea ice and access to open water. Unconsolidated pack ice drifts constantly, facilitating unrestricted movements to new feeding areas and haul-out sites, and enabling a large population of walruses to overwinter (Fay et al. 1984). In contrast, polynyas are much smaller than overwintering areas in pack-ice, and limit the ability of walruses to move during late winter (February and March). Because of this, only a relatively small number of walruses would be expected to overwinter in a polynya, such as the one at Dundas Island. In this paper I estimate the number of walruses overwintering in the Dundas polynya and Penny Strait region during the late winter, determine the distribution of walruses relative to sea-ice conditions, assess fidelity to overwintering sites, comment on the amount of time individual males spend in the polynya, and document the size and composition of walrus herds.

5.2 MATERIALS AND METHODS

Twenty aerial surveys of the coastal regions along Pioneer Channel, Couch Passage, Queens Channel and Penny Strait were completed between 22 March and 15 May from 1987-1989 (Figs. 5-1 and 5-2). Although the exact route varied between surveys depending on the location of walruses, amount and location of open water, ice conditions and weather conditions, the same general area was covered each time. After surveying the area north of Dundas Island, the route followed the coastline north of Cape Becher to Sir John Barrow Monument, Cape Sir John Franklin, and then on to Pioneer Island. The return trip included John Barrow Island, Hyde Parker Island, and the Cheyne Islands (Figs. 5-1 and 5-2). All areas near coastal islands, particularly Fairholme, Kerr, and Cracroft, were checked thoroughly for signs of walrus activity. If weather conditions deteriorated during the survey and it was not possible to cover the entire route, then areas near Dundas Island and between Cape Becher and Cape Sir John Franklin were given priority. Aircraft availability and weather conditions influenced the timing of surveys, but an effort was made to conduct at least two complete surveys per season. Survey dates and coverage are summarized in Table 5-1. The area around Crozier Island, Des Voeux Island, the Cheyne Islands, and John Barrow Island was surveyed on 27 April, 1989.

All surveys were flown in a Bell-206B helicopter. Two observers were present on each survey; one in the left front seat and one in the right rear seat behind the pilot. Survey altitudes varied from 80 to 150 m and ground speed varied from 90 to 110 km/hr depending on visibility and weather conditions. Data on number and location of walruses on the ice were recorded on a map and in a notebook. Where walrus numbers were high, data were recorded on a hand-held cassette recorder. A general description of sea-ice conditions along the route was recorded directly on a map and specific information on the type of sea ice at haul-out sites was documented in a notebook or on the cassette recorder. The classification scheme for describing sea-ice conditions is summarized in Table 5-2.

In 1987 and 1988, nine males were immobilized and branded with a two-digit, 12.5 cm high number on their hip and shoulder (Stirling and Sjare 1988). The brands were made with copper cattle irons heated with a propane torch. They were clearly visible at 500 m with a spotting scope and could be seen in enlargements of photographs taken from a helicopter at an altitude of approximately 100 m. The permanently marked males provided data on the fidelity of individuals to particular overwintering and breeding areas and on their seasonal movements. Locating suitable walruses to brand when weather conditions were conducive for immobilization was time-consuming, and conflicted with allocation of aircraft time for surveys of distribution and abundance. Consequently, fewer full coverage surveys were flown in 1987 and 1988 as compared to 1989.

The numbers of walruses hauled out on sea ice or seen swimming in the Dundas polynya were counted from an observation hut located on the top of a 80-m high cliff. Observations were made using a 15 to 60 power zoom spotting scope and 7 x 35 power binoculars from the windows of the hut. When weather conditions permitted, scans of the entire polynya were made every two hours during the daylight hours (in February and early March from approximately 1000 to 1600 and later in the season from 0730 to 2300). Data on the number of herds hauled out, an estimate of the number of walruses in each herd, and the locations of the herds, were noted. On days when visibility was poor, scans were made whenever possible. Observing and recording individual walruses or a herd of walruses was given priority over collecting haul-out data. However, even when walruses were in the immediate vicinity of the observation hut, at least two scans were completed each day.

A limited amount of data on sex and age composition of herds in the area around Dundas Island polynya and Fairholme Island are presented. These data were collected when herds were approached at close range for immobilization and branding or during aerial surveys. The characteristics used to sex and age walruses included the shape and size of the tusks, development of the neck and shoulder muscles, extent of blubber deposition in the upper neck region, and development of tubercles (Fay 1982). Walruses aged 1 to 3 years and associated with females were called calves. Male walruses aged 4 to 8 years were called juveniles, those aged 9 to 15 years, young adults, and those older than 15 years, mature males (Fay 1982).

5.3 RESULTS

5.3.1 Abundance of walruses in Penny Strait and the Dundas Island polynya based on aerial surveys and cliff-top counts

The maximum cliff top count of walruses hauled out or swimming in the Dundas polynya was 49 on 20 April 1987, 64 on 22 February 1988, and 24 on 22 February 1989. Daily counts were highly variable, and only a small proportion of the overwintering population was observed on any one day (Table 5-3). The mean daily number of walruses observed in the polynya area in 1988 ($\bar{x}=20.0$, SD=16.3, n=60) was significantly higher than in 1987 ($\bar{x}=9.8$, SD=10.7, n=47) or 1989 ($\bar{x}=7.3$, SD=5.8, n=66; KW test $p<0.0001$, Tukey test $p<0.05$). At least one walrus was seen on 45 of 55 observation days in 1987, on 60 of 69 days in 1988, and on all 66 days in 1989. Cliff-top observations provided the highest estimate of walruses present at the polynya in 1988 and 1989, while the greatest number of walruses seen in 1987 was during an aerial survey on 19 April (Table 5-1). Maximum herd size observed from the cliff-top was 35 in 1987, 28 in 1988 and 12 in 1989. The frequency of occurrence of different-sized herds varied significantly between years (G-test, $p<0.0001$, DF=10, n=140, 328, 226). A greater number of single walruses and fewer large herds (>5 walruses) were seen in 1989 than in 1987 or in 1988. There were no differences in the occurrence of different-sized herds between 1987 and 1988 (G-test, p=0.24, DF=5, n=140, 328). In 1989, approximately 46% of the herd sightings were of walruses in the water. Although swimming walruses were observed in 1987 and 1988, they accounted for less than 10% of the sightings in each year. This difference was due to the location of the polynya, ice conditions, and the distribution of the walruses. To ensure that all years were comparable, those herds that were observed in 1989, but could not have been observed in 1987 or in 1988, were dropped from the data set. However, even with this adjustment, there were still more single walruses and fewer large herds were sighted in 1989 than in 1987 or 1988 (G-test, $p<0.0001$, DF=8, n=140, 328, 128; Figure 5-3).

A total of 20 partial or full surveys were made of the Penny Strait region (including areas near Fairholme Island, Spit Island, John Barrow Island and the Cheyne Islands) and of the Dundas polynya from 1987 to 1989 (see Figure 5-2). The maximum number of walruses observed on a single day was 131 in 1987, 85 in 1988, and 67 in 1989 (Table 5-1). The total count for 1988 increases to 108 if one takes into consideration that there were at least 64 walruses residing in the Dundas polynya rather than the 42 counted on the survey (Table 5-3 on 22 February). The total count for 1989 increases to 115 if walruses seen at the Cheyne Islands and near Hyde Parker Island on 27 April are included, as well as, the 24 walruses overwintering at the Dundas Island polynya (Table 5-3 on 22 February).

Although data on the herd size and sex and age composition were limited, some patterns were noted (Table 5-4). During the late winter and early spring all lone walruses (n=6), pairs (n=9), and small herds with less than five walruses (n=10), were males. Herds composed of females, calves and immatures varied in size from 12 to 35 ($\bar{x}$=23.3, SD=10.2, n=4). Some larger all-male herds of 6 to 12 walruses ($\bar{x}$=9.0, SD=2.8, n=5) were also observed. The age structure of both small (<5) and larger all-male herds was mixed. Herds of similar size and sex and age composition were seen at Dundas Island and at Fairholme Island.

5.3.2 Resightings of marked walruses

A total of nine sexually mature male walruses were branded: seven in 1987 and two in 1989. Table 5-5 summarizes the dates and locations where each male was branded and subsequently resighted. Six of nine walruses were resighted one year after branding, and 3 were resighted in two consecutive years after branding. Males branded near Dundas Island were resighted swimming in the Dundas polynya or hauled out within 8 km of the location where they were originally branded. The two males branded in 1987 near Kerr Island, BR33 and BR34, were each resighted at least once during the spring in 1988 and 1989, and each time they were within 5 km of where they were originally branded. Male BR34 was also resighted on 12 August 1988, at a traditional summer haul-out site located on the southeast coast of Bathurst Island (135 km south of the location where he was branded). Males BR04 and BR44 were members of the same herd when branded and were resighted together on 21 April and 25 April 1988. Males BR33 and BR34 were also members of the same herd when branded and were resighted in herds that were hauled-out less than 200 m apart on 02 April 1989.

5.3.3 Sea-ice conditions in the Penny Strait region and Dundas Island polynya

The sea-ice conditions in the vicinity of the Dundas Island polynya, and the size and location of the polynya itself, varied seasonally. In February and March the polynya extended 0.5 to 2.0 km east to west, and 0.1 to 4.0 km north to south. During April and May, it increased to four or five times its initial size as large pans and chunks of annual ice broke away from its edges. The southern ice edge of the major body of open water was usually located within 1 km of Cape Collins; as spring approached, the polynya expanded to the west, northwest and north. However, in one year, 1987, the major body of open water was 5 km northwest of Cape Collins. The open water was surrounded by smooth pans of recently frozen ice, rough annual ice interspersed with older and thicker annual ice or multi-year ice pans (MYIPs), and rough pressure ice. Ice in the Dundas Island bay between Point Little and Cape Collins was solid, thick (>1.5 m thick), and relatively smooth as compared to the ice in Pioneer Channel; there was a noticeable shear zone between the two areas (Figure 5-1). MYIPs of various sizes ranging from 20 to 100 m in diameter were observed in the bay. There was also a noticeable shear zone running roughly north-south between Point Little and Cape Becher; the annual ice to the west was solid, and smooth as compared to ice closer to the polynya. To the north of Point Little the ice was thinner and was the first to breakup in the early spring. Although the only open water visible in the late winter was located in the immediate vicinity of the polynya, thin ice, cracks, and pockets of open water drifted over by snow were present at the base of large pressure ridges and along the edges of MYIPs throughout the area.

The predominant sea ice type along the survey route north of Cape Becher was smooth, annual landfast ice with little or only moderate pressure ridge or ice hummock development. However, some locations along the route did exhibit other types of ice and ice features that were noticeably different and were relatively consistent each year. Along the coast just north of Cape Becher, the ice had larger and more numerous networks of pressure ridges than the coastline in the Sir John Barrow Monument area. The ice in the mouth of Inglis Bay was always smooth with no ridging or hummocks. There were three locations along the shoreline approximately 10 to 15 km south of Sir John Barrow Monument where small (< 20 m dia) MYIPs consistently occurred (Figure 5-2). A characteristic feature of the ice in the Fairholme Island area was the presence of 10 to 50 m dia MYIPs pushed up against the shoreline of the islands (particulary off prominent tips of land or capes) and in the passage between the islands and the Grinnell Peninsula. Areas of thin, smooth annual ice were common around the south tip of Fairholme Island, the west arm of Kerr Island, and north of Cracroft Island. Recurring pressure ridges originate from the tips of some islands (particulary Fairholme) and run toward prominent capes on other Islands or to the Grinnell Peninsula. Ridged shoreline ice occurred where annual ice pans had been blown against one of the islands.

The distinguishing ice features between Cape Sir John Franklin and Pioneer Island were patches of thin, annual ice along the west coast and the south tip of Spit Island and the occurrence of many large (50 to 200 m dia) MYIPs north of Loney Point to Pioneer Island. The ice between Spit Island and John Barrow/Hyde Parker Islands, and from there south to the Cheyne Islands was smooth, with only occasional, well drifted pressure ridges. Within 2 km of both island complexes the ice was similar to that in the Fairholme Island area. Thin annual ice occurred between John Barrow and Hyde Parker Islands and off the northern tip of John Barrow and southern tip of Hyde Parker. Small (< 30 m dia) MYIPs were observed pushed up against the shoreline, but were not observed in nearby offshore areas. Ridged shoreline ice occurred on both islands. There were no noticeably thin patches of annual ice near the Cheyne Islands and pressure ridges were not as common as at the other island complexes. However, within approximately 800 m of the three small islands there were usually numerous MYIPs of various sizes (20 to 300 m dia) and much rough annual ice. Ice conditions from the Cheyne Islands to Cape Becher were variable. Although smooth, annual ice predominated, what looked like shear zones of rough pressure ice (approximately 1-2 km wide and of undetermined length) were sometimes observed. There were also large areas braided with a network of prominent pressure ridges.

5.3.4 The distribution of hauled out walruses in relation to sea-ice features

Walruses were not distributed randomly along the entire survey route during the late winter and early spring; some areas were used consistently throughout the spring in all years while others were never used. Although smooth, annual ice was the predominant ice type along most of the survey route (particularly north of Cape Becher), few walruses were observed in this habitat type. In 1987, 23 of 265 walruses were sighted in smooth annual ice, 31 of 170 in 1988, and none in 1989 (Table 5-6). Walruses in the Fairholme, John Barrow/Hyde Parker, and Cheyne Islands areas were all observed within 1.5 km of an island coastline. The major differences in the ice in these areas as compared to areas further offshore were the occurrence of MYIPs, areas of thin ice with cracks or pressure ridges, and the occurrence of rafted annual ice along the shores of the Islands.

The distribution of walruses in the vicinity of the Dundas Island polynya in early spring appeared to be influenced most by the location of thin ice and open water. During the late winter and early spring the highest numbers of walruses were observed in the patch of thin ice extending northward from Point Little or swimming in the polynya. By mid April they began to haul out in other areas of the polynya. The occurrence of thin ice, rough annual ice interspersed with smooth pans of annual or multi-year ice, and the presence of open water, contrasted greatly with sea-ice conditions in other areas of Penny Strait. Although few detailed observations of the ice conditions in Couch Passage between Baillie-Hamilton and Dundas Island were made, the conditions appeared to be similar to the area north of Dundas Island. Comparable data on the distribution of walruses in this area were not collected.

There may be important interrelationships between sea-ice features, herd size, and the sex or age of walruses using a haul-out site. In the Fairholme Island area from 1987 to 1989, 26 walruses were observed singly or in herds at cracks and pressure ridges. Herd size was less than 5 in all cases (mode=1) and all walruses were known or presumed males. Known females with calves or presumed females were not observed to use haul-out sites at cracks and pressure ridges late in the winter. There were six sightings of 24 walruses hauled out along the interface between ridged shoreline ice and the smooth annual ice lying offshore. The herds varied in size from 1-11 (median=3, $\bar{x}=4.0$, SD= 3.6, n=6) and were all-male. Again, no herds with females and calves used this type of sea ice. The few large herds containing females and calves that were observed, used a haul-out site along the edge of a MYIP or a site in thin, relatively smooth annual ice. In both cases the haul-out site was usually located 0.50 to 1.5 km from the coastline of an island.

5.4 DISCUSSION

5.4.1 Abundance of walruses

Estimating the abundance of walruses in an area is difficult because the haul-out behavior of walruses is usually synchronous and it is not possible to determine what proportion of the population is underwater (Estes and Gilbert 1978; Fay 1982; Gilbert 1989; Hills 1992). The factors that influence the timing of haul-out are not well enough understood to correct for this problem (Hills 1992). The best estimates of walrus abundance in the vicinity of the Dundas Island polynya during late winter and early spring each year resulted from a combination of daily cliff-top counts of walruses hauled out on the ice or swimming in the polynya, plus periodic aerial surveys. Even with these frequent counts, it was not possible to relate the accuracy of the maximum number of walruses observed to the total population. Consequently, the maximum counted at any time can only be regarded as a minimal estimate. This is particulary true for the 1988 and 1989 cliff top counts. Although it was not possible to quantitatively compare cliff-top counts with aerial counts of the polynya, it was clear that observers underestimated the size of herds with more than 15 walruses and that some walruses hauled out behind pressure ridges where they could not be seen from the hut. The maximum number of walruses counted in the polynya area each year occurred between 22 February and 19 April. At this time, ice in areas adjacent to the polynya had not started to breakup so it was unlikely that any walruses had immigrated or emigrated from the area. Walruses counted between those dates probably overwintered in the polynya. Daily counts dropped during late April and May in all three years; as spring breakup proceeded walruses may have dispersed.

Assuming that the maximum cliff-top count obtained for each year is a reasonable minimum estimate of the total number of walruses overwintering in the Dundas polynya, then it is possible to approximate what proportion of the estimated total population hauled out on any one day. The maximum daily count was less than 30% of the estimated total on 56 to 77% of the scan days over a three year period. Counts exceeding 70% of the estimated population were made on only 9 to 11% of the scan days. These data emphasize how variable the daily counts were and how difficult it is to census walruses.

The factors that determine how many walruses overwinter in the polynya are unknown. For example, the polynya was larger in 1989 than in 1987 or 1988, but fewer walruses were present. Perhaps the timing and progression of freeze-up early in the winter has a significant influence on the distribution of walruses in the polynya and surrounding regions. Sufficiently detailed information on the number, density, and distribution of Atlantic walruses overwintering in other areas of the Canadian Arctic or Greenland is not available for comparison. However, densities of Pacific walruses overwintering in the drifting pack ice of the Bering Sea, may be up to two orders of magnitude greater than at the Dundas Island polynya (Fay et al. 1984).

Obtaining an estimate of the number of walruses overwintering in the entire Penny Strait region (including Dundas Island) on the basis of aerial surveys was equally difficult. Davis et al. (1978) observed 81 walruses on 19 April and 189 on 17 June, 1977. Since the ice to the south and north of the survey area was still solid in June the authors believed that no walruses had moved into or out of Penny Strait during the interval between surveys, and that the increase in numbers was due to an increase in the proportion hauled out. On the basis of these data they concluded that approximately 200 walruses overwintered in the Penny Strait region. The maximum numbers of walruses counted on a single survey of the same area in the early spring of 1988 and 1989 were reasonably close to the result obtained by Davis et al. (1978). However, the maximum number of walruses seen in 1987 was higher than in 1977 (131 compared to 81). When the highest survey counts of 1988 and 1989 were adjusted to include the maximum number of walruses seen in each area (Dundas Island, Fairholme Island, John Barrow Island, and the Cheyne Islands) the minimum population estimates increased to 108 and 115 respectively. The number of walruses counted on the 19 April survey in 1987 was the highest estimate of the minimum number of animals in Penny Strait during the survey period. Thus, the estimates of walruses overwintering in Penny Strait over a three-year period were reasonably consistent. The region may be able to support only a limited number of walruses through the winter. The restricted accessibility of food due to ice cover during the winter months is probably the most critical factor limiting their numbers (Fay 1982). There are no data on the distribution and abundance of species eaten by walruses in the study area. Because no surveys were completed in June during this study it is not possible to comment on what proportion of the population was accounted for in the early spring. However, given the consistency of the maximum estimates for this study and the similarity of these data compared with data collected in 1977, it appears likely that there was an overwintering population of approximately 200 walruses in the Penny Strait region.

5.4.2 Comments on herd composition, size, and fidelity of walruses to an overwintering area

Although data on herd composition are limited, it is clear that single males, male herds of variable size, and large herds of females and calves frequent both the Dundas Island polynya and the Fairholme Island area. It was not possible to observe walruses in the Fairholme area for long enough periods to establish whether or not breeding activity occurred there. However, young adult and mature males were seen in the area, some of which had fresh wounds on their necks and shoulders. It was also common to see blood on the ice at haul-out sites, suggesting that males were fighting and that some competition for access to females was occurring.

Between-year variations in the frequency of occurrence of different-sized herds were apparent regardless of whether or not the 1989 observations were adjusted to account for walruses that would not have been seen in the other two years. A greater number of single walrus sightings and fewer herd sightings were made in 1989 than in 1987 and 1988. The low number of walruses (minimum estimate of 24) overwintering in the polynya in 1989 may partially explain these observations. However, the sharp decline in sightings of pairs of walruses, and herds of 3 to 10 walruses, suggests that other factors were important too. One or two large herds (12 to 35) of females overwintered at the polynya each year (Chapter 2). The other large herds (6 to 12) sighted in the area included predominantly young adult males. In addition, during the late winter and early spring only males have been observed to haul out in pairs (often a mature male and a juvenile or young adult) or triads (often a mature male and two younger males). Thus, a reduced number of juvenile and young adult males overwintering in the polynya could explain the observed differences in herd sizes.

Resightings of branded and distinctively scarred males indicate that at least some individuals returned to the same overwintering or breeding areas for two or three consecutive years. From 1987 to 1989 there were 23 young adult or mature males identified in the Dundas polynya. Six of these males (8305, 8805, BR11, BR04, BR44, and BR02; see Chapters 2 and 3 for data on non-branded but identified males) returned to the polynya at least once: 8805, BR04, BR44 and BR02 were sighted at the polynya one year after they were first identified while BR11 was sighted in two consecutive years. Male 8305 was seen in 1983, 1984, and 1987. This male was easily recognized and would have been noticed had he been in the area during 1985 and 1986. No walruses branded at Dundas Island were seen in the Fairholme Island area, or vice versa. The two males, BR33 and BR34, branded near Fairholme Island were both resighted within 5 km of the spot where they were originally branded in two consecutive years. Multiple sightings of branded males and other males with distinctive scars in the same areas indicate that once a male moves into an overwintering area, he remains there for an extended period of time (usually until spring breakup, see Chapters 2 and 3 for residence times of non-branded but identified males). On the basis of these observations it appears that movements of walruses between overwintering areas are limited and that most walruses show at least short-term fidelity to specific overwintering areas. Resightings of males that were in the same herd when branded and then were observed hauled out together one or two years later suggests that loose associations may exist between certain individuals within overwintering/breeding populations. It is possible these associations are an extension of the associations observed between singing and non-singing males swimming around the polynya area (Chapter 3).

5.4.3 Sea-ice conditions and the distribution of walruses

The primary criterion determining the distribution of walruses in the Penny Strait region north of the Dundas Island polynya was the reliable occurrence of thin annual ice, or other sea-ice features that allowed walruses access to open water. They use their tusks to scrape and chisel breathing or haul-out holes in the thin ice or to enlarge pockets of open water along cracks and at the bases of large pressure ridges. Open water or thin ice also occurred in the shear zone at the interface between the edge of a MYIP and the surrounding annual ice. The MYIPs are thicker than the surrounding ice and rock with the changing tides and ocean currents. Many are also grounded so that tidal action constantly raises and lowers the surrounding annual ice causing cracks to occur around the edges of the pan. Walruses maintained breathing and haul-out holes in this interface area. Tidal action also maintained cracks along the interface between ridged shoreline ice and the smooth annual ice. Thin annual ice, cracks, pressure ridges, ridged shoreline ice, and MYIPs occurred consistently around coastal island complexes along the survey route. These were the only areas where walruses were sighted, and all breathing holes and haul-out holes were associated with one or more of these sea-ice features.

For walruses overwintering in the Dundas polynya area it appeared that maintaining access to breathing holes and haul-out holes was easier since there was more open water and greater expanses of thin annual ice than in other areas of Penny Strait. Even so, walruses still sought out the thinnest ice and used MYIPs frequently. As spring breakup proceeded, the walruses moved into areas where there was thin rotting ice and open water. In 1982 and 1990 the Dundas Island polynya was very small (200 x 100 m) and few (2 seen in each year) walruses were in the area (Stirling unpublished data and personal observation). In 1985 the polynya was extremely large (8.0 x 6.0 km) late in the winter and, again, there were few walruses near Dundas Island (Stirling unpublished data). Thus, even when open water and ice suitable for breathing and haul-out holes appeared to be more accessible than in areas to the north, the distribution of overwintering walruses in the Dundas Island polynya was variable and influenced significantly by sea-ice conditions.

Although the observations were limited, it appeared that lone males and small herds of males frequently hauled out at pressure ridges, cracks, and along the interface of ridged shoreline ice, while herds of females and calves used MYIPs or thin annual ice in areas where their vision was less obscured by large pressure ridges or land. It is likely that potential predation by polar bears is a critical factor in determining where a herd of females will haul out. Because of their large size, walruses older than approximately 4 years of age do not often fall prey to bears unless they are sick or get frozen out of their haul-out hole. Calves are probably taken more frequently (Fay 1982; Calvert and Stirling 1990). When a bear charges a herd of hauled-out walruses the calf may get separated from its mother in the confusion. By hauling out at locations where it would be difficult for a bear to approach without being detected, females could significantly reduce the risk of predation. Herds of females with calves are more vigilant than males (personal observation) which is consistent with the hypothesis that they experience greater predation pressure than males.

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Table 5-1. Summary of numbers, herd size and general location of walruses observed during surveys from 1987-1989.

Date (d/m/y)	Survey coverage	Areas not surveyed	Number of walruses seen	Number of walrus sightings	Mean herd size (SD) and Range	% of walruses seen at each location (n)	Location of walruses sighted
25/03/87	Full		0	0			
04/04/87	Partial	N of C Sir J. Franklin	30	8	4.3 (5.3) (1-12)	3 (1/30)	Dundas I
						7 (2/30)	Fairholme I
						43 (13/30)	Kerr I
						3 (1/30)	Toms I
						3 (1/30)	Hyde Parker I
						40 (12/30)	Cheyne Is
19/04/87	Full		131	17	8.4 (9.1) (1-35)	44 (57/131)	Dundas I
						36 (11/131)	Fairholme I
						5 (6/131)	Kerr I
						12 (16/131)	Toms I
						3 (4/131)	Cracroft I
						5 (6/131)	Spit I
						1 (1/131)	Hyde Parker I
						23 (30/131)	Cheyne Is
26/04/87	Partial	N of C Becher	21	3	6.7 (8.1) (2-16)		Dundas I
27/04/87	Partial	N of Kerr I Hyde Parker I Cheyne Is	44	12	3.7 (2.6) (1-10)	59 (26/44)	Dundas I
						32 (14/44)	Fairholme I
						9 (4/44)	Kerr I
02/05/87	Partial	N of C Sir J. Franklin Hyde Parker I Cheyne Is	29	8	3.6 (3.1) (1-11)		Dundas I
03/05/87	Partial	N of Fairholme I	51	14	3.8 (1.7) (1-7)	31 (16/51)	Dundas I
						18 (9/51)	Fairholme I
						33 (17/51)	Kerr I
						18 (9/51)	Cheyne Is
08/05/87	Partial	N of Cape Becher Hyde Parker I Cheyne Is	20	7	2.9 (2.9) (1-8)		Dundas I
12/05/87	Partial	N of Fairholme I Hyde Parker I Cheyne Is	31	10	3.4 (2.5)	45 (14/31)	Dundas I
						36 (11/31)	Fairholme I
						13 (4/31)	Kerr I
						7 (2/31)	Toms I
16/05/87	Partial	N of C Becher	39	11	3.5 (2.2) (1-7)		Dundas I
02/04/88	Partial	N of Spit I Cheyne Is	5	2		80 (4/5)	Dundas I
						20 (1/5)	Kerr I

Date (d/m/y)	Survey coverage	Areas not surveyed	Number of walruses seen	Number of walrus sightings	Mean herd size (SD) and Range	% of walruses seen at each location (n)	Location of walruses sighted
25/03/87	Full		0	0			
15/04/88	Partial	N of Spit I	85	12	7.08 (7.8)	49 (42/85)	Dundas I
		John Barrow I			(1-28)	33 (28/85)	Fairholme I
		Hyde Parker I				14 (12/85)	Kerr I
		Cheyne Is				4 (3/85)	Spit I
17/04/88	Partial	N of Kerr I	49	15	3.3 (2.7)	14 (7/49)	Dundas I
					(1-12)	51 (25/49)	Fairholme I
						33 (16/49)	Kerr I
						2 (1/49)	John Barrow I
21/04/88	Partial	N of C Becher	40	6	6.6 (7.7)		Dundas I
		John Barrow I			(1-18)		
		Hyde Parker I					
		Cheyne Is					
01/05/88	Partial	N of C Becher	14	3	4.7 (3.2)		Dundas I
		John Barrow I			(1-7)		
		Hyde Parker I					
		Cheyne Is					
02/05/88	Partial	N of C Becher	15	4	3.8 (2.9)		Dundas I
		John Barrow I			(2-8)		
		Hyde Parker I					
		Cheyne Is					
09/05/88	Partial	Cheyne Is	50	13	3.8 (4.3)	14 (7/50)	Dundas I
					(1-15)	30 (15/50)	Fairholme I
						6 (3/50)	Kerr I
						44 (22/50)	Cracroft I
						6 (3/50)	Spit I
22/03/89	Full		0	0			
02/04/89	Partial	Cheyne Is	67	10	6.7 (8.7)	45 (30/67)	Fairholme I
					(1-30)	27 (18/67)	Kerr I
						3 (2/67)	Hyde Parker I
						18 (12/67)	Spit I
						5 (3/67)	Toms I
						3 (2/67)	Dundas I
21/04/89	Partial	Cheyne Is	39	11	3.5 (3.5)	39 (15/39)	Fairholme I
					(1-10)	13 (5/39)	Kerr I
						18 (7/39)	Spit I
						26 (10/39)	Hyde Parker I
						5 (2/39)	Dundas I

Table 5-2. Definitions of ice features and ice types.

Ice feature/type	Description
Pressure ridge	A ridge of ice caused when a large pan of ice buckles under pressure or when two pans collide and ice is pushed up along the edges of the pans where contact is made. The ridges can vary in size from < 1 - 6 m.
Multi-year ice pans	A pan of ice (usually 10 - 200 m in diameter) that is at least three years old. These pans are thick (>2 m), eroded and differ in color from annual ice or second year ice.
Ridged shoreline ice	Annual ice that has been blown or pushed by other ice sheets up against the shoreline. The ice breaks into large blocks and forms a distinct ridge. Many of the blocks are grounded.
Type 1	Smooth annual ice. Solid, stable fast ice (ice that is attached to land) with only occasional pressure ridges. The ridges have a linear appearance.
Type 2	Rough annual ice. Same as above except that there are a moderate number of pressure ridges that create a rougher appearance to the ice. The pressure ridges form a complex network of variably shaped polygons.
Type 3	Rough pressure ice. Annual ice that has been broken and crushed into rubble and then refrozen. There is no distinct pattern of pressure ridges.

Table 5-3. Summary of daily numbers of walruses seen hauled out on ice near Dundas Island 1987-1989.

Date (d/m)	1987		1988		1989	
	Number of walruses counted	% of total est. number of walruses	Number of walruses counted	% of total est. number of walruses	Number of walruses counted	% of total est. number of walruses
09/02					1	4
10/02					3	13
11/02					6	25
12/02					11	46
13/02					3	13
14/02			0*		14	58
15/02			NS**		2	8
16/02			0		3	13
17/02			2	31	8	33
18/02			0		1	4
19/02			NS		21	88
20/02			0		11	46
21/02			0		12	50
22/02			0		24	100
23/02			NS		10	42
24/02	NS		0		4	17
25/02	NS		64	100	3	13
26/02	NS		29	45	19	79
27/02	NS		2	3	11	46
28/02	0		7	11	15	63
29/02			14	22		
01/03	0		0		NS	
02/03	NS		25	39	11	46
03/03	NS		0		15	63
04/03	1	2	2	3	7	29
05/03	NS		0		18	75
06/03	NS		14	22	12	50
07/03	5	10	0		16	66
08/03	17	35	35	55	17	71
09/03	NS		45	70	NS	
10/03	6	12	11	17	NS	
11/03	NS		42	66	3	13
12/03	13	27	0		13	54

	1987		1988		1989	
Date (d/m)	Number of walruses counted	% of total est. number of walruses	Number of walruses counted	% of total est. number of walruses	Number of walruses counted	% of total est. number of walruses
13/03	NS		15	23	7	29
14/03	11	23	24	38	16	67
15/03	35	71	6	9	8	33
16/03	3	6	0		1	4
17/03	4	8	NS		2	8
18/03	0		0		5	21
19/03	0		28	44	7	29
20/03	NS		10	15	6	25
21/03	0		NS		3	13
22/03	1	2	NS		8	33
23/03	0		13	20	14	58
24/03	3	6	24	38	13	54
25/03	NS		7	11	4	17
26/03	0		64	100	3	13
27/03	36	74	22	34	2	8
28/03	13	27	6	9	NS	
29/03	0		8	13	NS	
30/03	10	20	6	9	3	13
31/03	10	20	10	16	2	8
01/04	14	29	60	94	3	13
02/04	6	12	NS		3	13
03/04	5	10	19	30	7	29
04/04	2	4	20	31	5	21
05/04	4	8	12	19	2	8
06/04	1	2	17	27	4	17
07/04	2	4	7	11	3	13
08/04	1	2	NS		2	8
09/04	3	6	63	98	1	4
10/04	NS		9	14	3	13
11/04	17	35	NS		2	8
12/04	20	41	37	58	5	21
13/04	16	33	57	89	2	8
14/04	11	22	21	33	NS	
15/04	15	31	41	64	3	13
16/04	NS		10	16	3	13
17/04	NS		13	20	1	4

	1987		1988		1989	
Date (d/m)	Number of walruses counted	% of total est. number of walruses	Number of walruses counted	% of total est. number of walruses	Number of walruses counted	% of total est. number of walruses
18/04	44	90	9	14	5	21
19/04	NS		13	20	4	17
20/04	49	100	22	35	17	71
21/04	8	16	24	37	NS	
22/04	0		10	16	8	33
23/04	0		3	5	0	
24/04	11	22	24	38	0	
25/04	6	12	8	13	0	
26/04	NS		14	22	0	
27/04	4	8	12	19	0	
28/04	7	14	31	48	0	
29/04	4	8	1	2	0	
30/04	NS		13	20		
01/05	NS		10	16		
02/05	NS		14	22		
03/05	NS		0			
04/05	7	14	32	50		
05/05	NS		16	25		
06/05	NS		15	23		
07/05	3	6	0			
08/05	3	6	9	14		
09/05	7	14				
10/05	1	2				
11/05	15	31				
12/05	1	2				
13/05	7	14				
14/05	5	10				
15/05	3	6				
16/05	2	4				
17/05	4	2				
18/05						
19/05						
20/05						

* scanned but nothing was seen; ** no scans

Table 5-4. Summary of herd size and sex/age composition of walruses hauled out in Penny Strait region 1988-1989.

Survey date (d/m/y)	Number of herds with known sex and/or age composition (n)	Herd size and sex and/or age composition of each herd	Location of each herd
02/04/88	2 (2)	4 males	D*
		1 male	F**
15/04/88	4 (12)	2 males	D
		23 F/C, JUV	D
		2 males	F
		1 male	F
17/04/88	13 (15)	1 male	D
		4 males	D
		3 males	D
		1 male	F
		3 males	F
		2 males	F
		12 F/C, JUV	F
		2 males	F
		2 males	F
		3 males	F
		4 males	F
		2 males	F
		3 males	F
21/04/88	5 (6)	1 juv	D
		2 males	D
		2 YAM	D
		18 JUVS	D
		12 JUV, YAM, males	D
01/04/88	2 (3)	1 male	D
		6; (1) JUV, (2) YAM, 3 males	D
02/04/88	3 (4)	2 males	D
		8 JUV, YAM, males	D
		3; (1) JUV, (2) males	D
02/04/89	4 (10)	4; (1) YAM, (3) males	F
		7; (2) JUV, (1) YAM, (4) males	F
		3; (2) YAM, 1 male	F
		35 F/C, JUV	F
27/04/89	1 (11)	12; (2) JUV, (5) YAM, (5) males	C***

F/C females and calves; JUV juveniles; YAM young adult males

* Dundas Island area

** Fairholme Island area

*** Cheyne Island area

Table 5-5. Dates and locations of brandings and resightings of branded walruses 1987-1989.

Brand identification	Date (d/m/y) and location of branding	Date (d/m/y) and location of first resighting	Date (d/m/y) and location of second resighting	Date (d/m/y) and location of third resighting	Date (d/m/y) and location of fourth resighting
00	06/05/87 Dundas Is.				
11	06/05/87 Dundas Is.	25/04/88 Dundas Is.	05/03/89 Dundas Is.	08/03/89 Dundas Is.	
22	08/05/87 Dundas Is.	16/05/87 Dundas Is.			
33	12/05/87 Kerr Is.	09/05/88 Kerr Is.	02/04/89 Kerr Is.		
34	12/05/87 Kerr Is.	15/04/88 Kerr Is.	17/04/88 Kerr Is.	21/08/88 Bathurst Is.	02/04/89 Kerr Is.
04	16/05/87 Dundas Is.	16/04/88 Dundas Is.	21/04/88 Dundas Is.	25/04/88 Dundas Is.	
44	16/05/87 Dundas Is.	21/04/88 Dundas Is.	02/05/88 Dundas Is.		
02	16/04/88 Dundas Is.	19/02/89 Dundas Is.	08/03/89 Dundas Is.		
01	16/04/88 Dundas Is.	25/04/88 Dundas Is.			

Table 5-6. Summary of sea-ice features associated with occupied haul-out sites observed during surveys 1987-1989.

Year	Dates of surveys (d/m)	Number of walruses observed	Number of walruses observed at haul-out sites with known ice conditions	Percentage of walruses hauled out at sites near specific sea ice features (n)	Ice features
1987	04/04, 19/04, 27/04 02/05, 03/05, 12/05	316	265	57 (150/265)	edge of a MYIP[*]
				29 (78/265)	rough, annual polynya ice
				9 (23/265)	smooth, solid annual ice
				5 (13/265)	along a pressure ridge
				0 (1/265)	jumbled, annual shore ice
1988	02/04, 15/04, 17/04 21/04, 01/04, 01/05 02/05, 09/05	258	170	21 (35/170)	edge of a MYIP
				18 (31/170)	rough, annual polynya ice
				22 (38/170)	smooth, solid annual ice
				4 (6/170)	along a pressure ridge
				17 (29/170)	jumbled, annual shore ice
				14 (24/170)	rotten, smooth annual ice
1989	02/04, 21/04, 27/04	149	137	89 (122/137)	edge of a MYIP
				3 (4/137)	rough, annual polynya ice
				2 (2/137)	along a pressure ridge
				4 (5/137)	along an open crack
				3 (4/137)	rotten, smooth annual ice

[*] MYIP multi-year ice pan

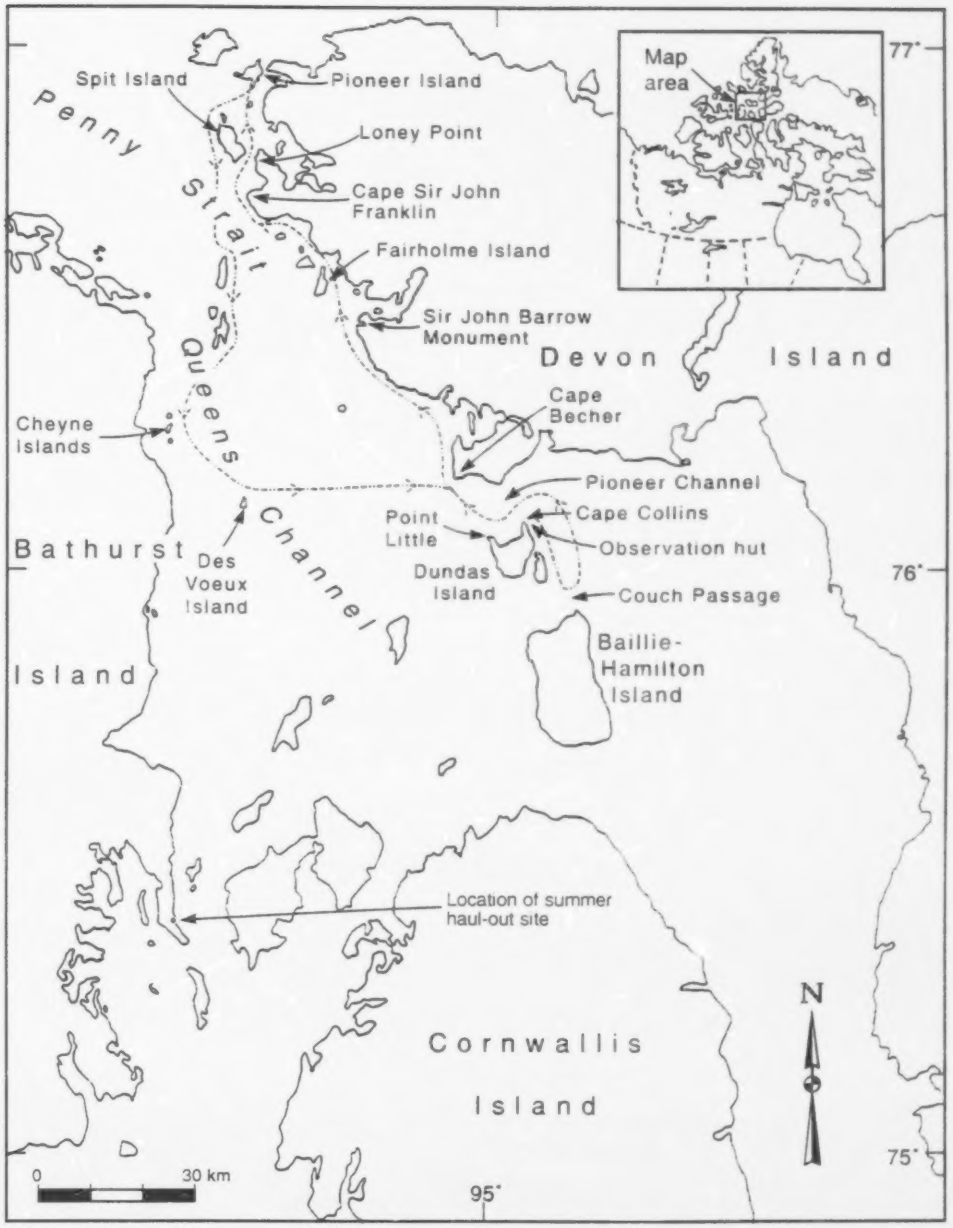
Spit Island
Pioneer Island
Penny Strait
Loney Point
Cape Sir John Franklin
Map area
77°
Fairholme Island
Sir John Barrow Monument
Devon Island
Queens Channel
Cheyne Islands
Cape Becher
Pioneer Channel
Cape Collins
Point Little
Observation hut
Bathurst Island
Des Voeux Island
Dundas Island
Couch Passage
76°
Baillie-Hamilton Island
Location of summer haul-out site
N
Cornwallis Island
0
30 km
95°
75°

Figure 5 - 1. Map of the study area, showing the general survey route.

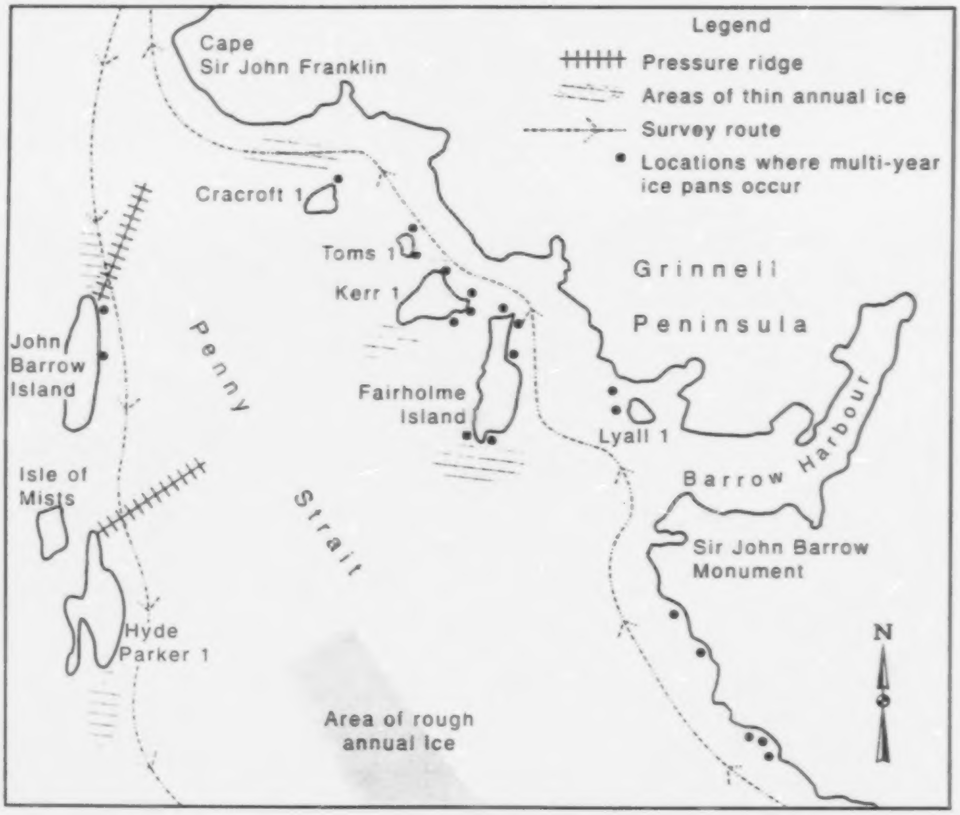
Legend
Pressure ridge
Areas of thin annual ice
Survey route
Locations where multi-year ice pans occur
Cape Sir John Franklin
Cracroft 1
Toms 1
Kerr 1
Grinnell Peninsula
John Barrow Island
Penny Strait
Fairholme Island
Lyall 1
Barrow Harbour
Isle of Mists
Sir John Barrow Monument
Hyde Parker 1
Area of rough annual ice
N

Figure 5 - 2. Detailed map of the area near Fairholme Island. Major ice features are shown.

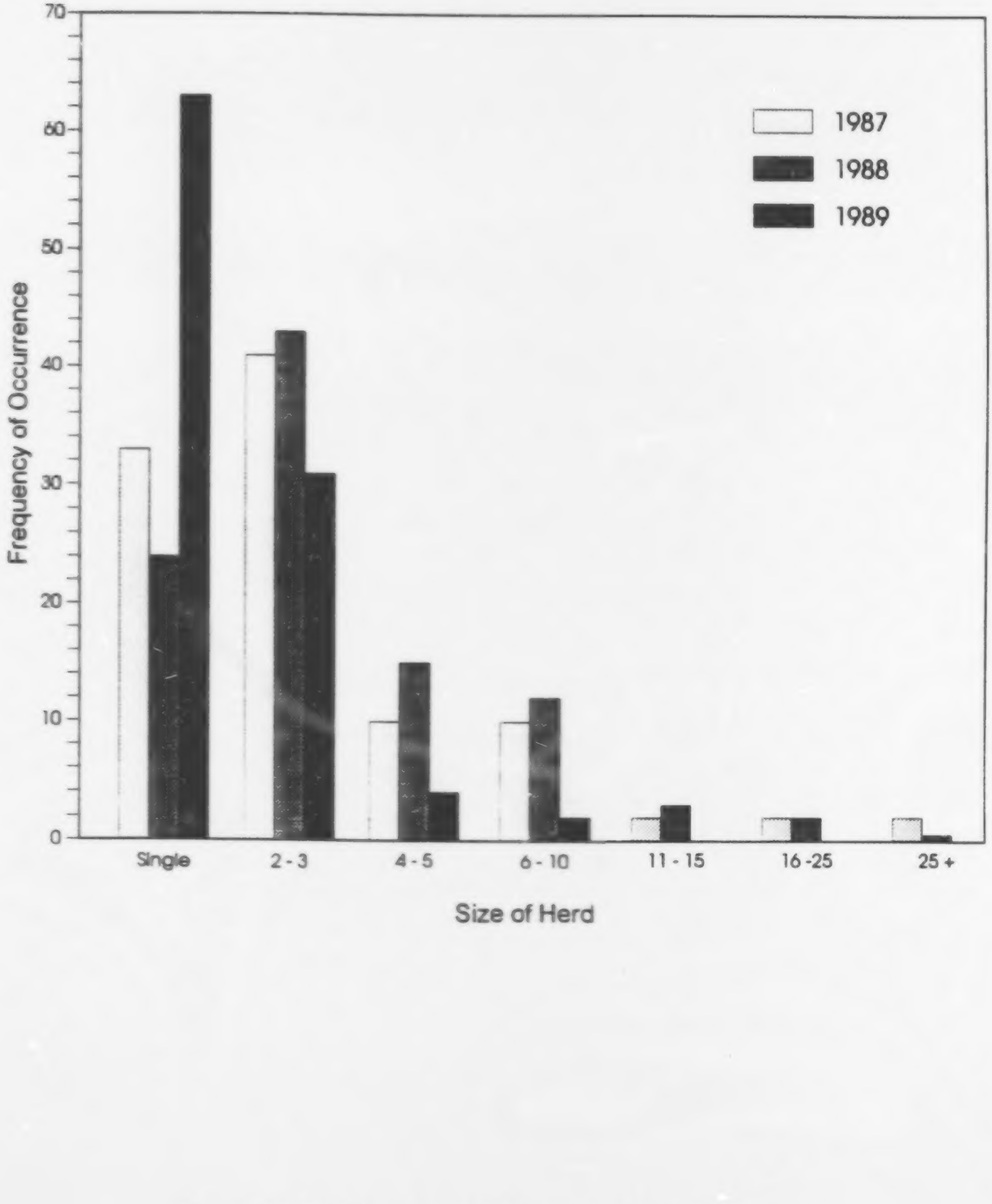

Figure 5-3. Frequency of occurrence of different-sized herds in 1987, 1988, and 1989.

6. GENERAL CONCLUSIONS

Although most ice-breeding pinnipeds exhibit low levels of polygyny and are thought to be promiscuous or have a serially monogamous mating system (Stirling 1983; Boness 1991), Atlantic walruses overwintering and breeding in the Dundas Island polynya and nearby areas have a moderately polygynous female-defense mating system. The most important factor facilitating this form of mating system in walruses appears to be female gregariousness, a social condition lacking in most other pagophilic species during the breeding season. Predator avoidance, increased foraging efficiency, and phylogenetic factors are thought to have influenced the evolution of gregariousness in females (Stirling 1975; Fay 1982; Taggart 1987). Regardless of which factor affected the evolution of gregariousness to the greatest extent, the consequence is that one male is able to monopolize access to several females at a time.

There appeared to be well established dominance relationships among males. Only large mature males (> 15 years of age) that sang extensively during the breeding season were successful in obtaining a position as an attending male and, of those males, one appeared to spend a greater proportion of time with a herd. Most attending males associated with a herd for approximately three days, but their residency time varied from one to five days. During his tenure, an attending male continuously repeated a stereotyped song and was the only male that initiated earnest sexual activity with females. His presence and behavior influenced the sexual and singing behavior of young adult male members of the herd and seemed to deter vocal satellite males from approaching closer than 50 to 100 m.

Little is known about the dynamics of a herd take-over except that, judging from fresh wounds on males, at least some interactions involved fighting. Once an attending male was displaced, his location and activities were largely unknown. In some cases a male became silent and remained near the herd; at other times he hauled-out for a brief period, and sometimes he sang elsewhere in the polynya.

The importance of female choice in determining which male gained access to a herd is unknown. However, females members of a herd were not observed to leave the group and associate with another male singing alone in the polynya. Additionally, lone females did not approach or consort with satellite males or lone singers in the polynya. Female gregariousness itself may be a subtle, indirect way of expressing choice (Beehler and Foster 1988). A herd with several oestrous females is likely to attract and perhaps incite competition among the most reproductively successful males.

The chances of a young adult male securing an attending male position appeared to be unlikely. Therefore, spending most of their time as silent herd members, as vocal satellite males, or alternating between the two behaviors may be the best strategy to maximize their immediate or future reproductive success. There were no obvious interactions between individuals that appeared to determine which strategy a male adopted. A male's behavior may be determined by his social status and by the identity and singing behavior of other males in the area at the time. Satellite males do not have the opportunity to associate closely with female members of a herd, but the more dominant individuals may be in a position to challenge an attending male and take over his herd. This is probably the most significant advantage of being a satellite male. Young adult male herd members have the opportunity to closely associate with females for an extended period of time and to shadow or closely monitor the behavior of the attending male. Both types of learning experiences could eventually enhance a young adult male's chances of becoming a dominant male.

Although there are only a few anecdotal observations of Pacific walruses during the breeding season, their mating system appears to be more like a lek than female defense (Fay et al. 1984). No one male monopolizes access to the herd. Instead, males actively defend small display territories near the herd and females have the opportunity to choose one of the displaying males as her mate (Fay 1982; Fay et al. 1984). Variations in the form of mating system and degree of polygyny between the two subspecies may be a result of different ice conditions (unconsolidated packice vs. polynya) in the overwintering area. In a polynya where the overwintering population is small and relatively sedentary due to restrictive ice conditions, males have the opportunity to interact with all potential competitors and to establish a dominance hierarchy. Because a herd composed of females is relatively small and its movements restricted, a dominant male is able to monopolize access to them. In the case of the Pacific walrus, a higher density of mobile males in the overwintering area may prohibit tight dominance relationships from becoming established, and may make it too energetically expensive for one male to control the behavior of all competitors. As a result, the most dominant males crowd closer to the females and aggressively defend small aquatic territories. With several large herds of relatively mobile females in an area males may opt to display near several herds for shorter periods of time rather than trying to continuously follow and defend one herd.

Mature male walruses in the Dundas Island polynya sang four main song types: a coda song, a DV song, an intermediate song, and an aberrant song. There are three consistent variations of the coda song and it is likely there are at least two consistent variations of the DV song. Both song types are extremely stereotyped and are shared by all males in the polynya. Their structures have not changed since 1981, but their proportions vary significantly between years (Stirling et al. 1983). Most males also sing intermediate and aberrant songs. Song structure varies within and between individuals. It is not known why certain song types or variations occur more frequently in some years than in others. It is possible that the songs of the most dominant males in a particular year influence what songs other males sing. The behavioral significance and function of non-stereotyped songs (erratic coda, intermediate and aberrant songs) are not known.

The duration and type (or variation) of song a male sang depended on his relative age and social status, the behavioral context in which he was singing, and the duration of the singing-bout. Not all factors affected all males to the same degree or in the same way. The factor that consistently caused significant changes in a male's song was the presence of females nearby. Attending males that were recorded in several different social contexts significantly abbreviated their songs, emitted more short coda songs, and spent more of their time at the surface when they were with females compared to when they sang alone. The behavioral significance of these changes are unknown. However, it is possible that attending males might shorten the underwater portion of their songs and spend more time at the surface to minimize possible interactions between young adult male herd members and females. Shortening the song also means that the number of full songs emitted per hour can increase significantly and that surface codas and diving vocalizations would be emitted more often. Given that surface codas (Chapter 4) and diving vocalizations (Stirling et al. 1987) may convey information on identity, short songs would allow an attending male to reinforce or advertise his identity to a greater extent.

In 1989, the repertoires of mature males that attended a herd (attending male) and of young adult males were significantly different from those of mature males that had never been observed to attend a herd. Total song duration differed between each of the categories of males as well. Attending and young adult males sang a greater number of short and erratic coda songs and fewer typical coda songs compared to mature males. Young adult males sang the shortest songs and mature adults the longest. The behavioral significance of these differences is not known. As the breeding season progressed and attending males spent more time with females singing short duration songs, it is possible that this trend carried over into times when they were singing alone.

Although a complete singing profile for any one male could not be constructed, it appeared that most mature males alternated between long, continuous bouts of singing and periods of rest for most of the breeding season. Based on a detailed singing profile of one male, the occurrence of song types (or variations) appeared to vary depending on whether they were emitted near the beginning, middle, or end of the singing bout. The male emitted fewer coda songs and a greater number of intermediate and aberrant songs as the singing bout progressed. Given the length of the singing bouts, one might expect that fatigue, and perhaps monotony, would be responsible (Hartshorne 1956, 1973; Kroodsma 1978).

Ray and Watkins (1975) suggested that walrus songs are primarily used to advertise the presence of a male in breeding condition and perhaps to establish an underwater territory or dominance hierarchy. In this study, there was no direct evidence that suggested songs functioned to attract females or establish an underwater territory. However, songs did appear to maintain dominance relationships (Chapter 2). It is not known for certain what vocal attribute(s) males were using to assess their opponent's social status, but the number of hours and days a male spends singing is likely to be an honest criteria (Clutton-Brock and Albon 1979). The length of a male's singing bouts relative to his rest periods during the breeding season probably reflect his overall condition (Le Boeuf 1972, 1988; Deutsch 1990; Boness 1991). Both inter- and intrasexual selection have probably shaped the evolution of walrus songs. However, on the basis of data presented in Chapter 2 and 3, it appears that intrasexual selection pressures may be more important. The dive pattern of a feeding walrus is remarkably similar to the dive pattern of a singing walrus. It is possible that the cyclic nature of feeding dives form the basis for the ritualized singing display (Tinbergen 1959; Alcock 1989).

Mature males varied the structure of their surface codas when singing in the presence of females, when there were loud background vocalizations, and with changes in date. As in the case of full song, not all factors affected all males to the same degree or in the same way. However, most males shortened their surface codas when singing in the presence of females and when background vocalizations were loud. They also emitted shorter surface codas closer to the beginning of the season compared with the end. Two males were recorded in more than one year; one male significantly changed his surface coda over a 4-year period, while the other male made only minor changes over 2 years.

Seven of the mature males emitted two distinct surface codas. The proportion of each variation emitted changed with date and year in which the walrus was recorded and whether the surface coda was emitted at the beginning or end of the surface portion of the song. It is not known why some males had two distinct codas and others did not: age or social status did not appear to be determining factors. A male that regularly alternated between two surface coda types was easier for the human ear to identify than a male with only one surface coda that closely resembled that of one or two other males. It would be difficult to experimentally determine how sensitive walruses are to such variation. Males younger than an estimated age of 10 years often emitted two or three variable surface codas and were not included in any analyses. In future studies it will be important to examine how surface codas develop and to determine when they become stereotyped.

Even though the structure of surface codas varied in response to a number of factors, there was sufficient individual variation to allow identification of walruses. Walruses that emitted two surface codas were treated as if they were two individuals. The two types were as distinctive from each other as they were from the surface codas of other individuals. Individual variation is a prerequisite for vocal recognition, but does not prove that surface codas function as individually distinctive vocalizations (Falls 1982). However, observations on the spacing behavior of singing males that were not in visual contact suggested that young adult males recognized the vocalizations of older, more dominant males, and either left the area or became silent when approached (Chapter 2). These observations support the idea that walruses listen to each other and that surface codas contain information on identity.

These conclusions are inferred from analyses of surface codas that were randomly sampled from all males singing in as many different behavioral situations as possible, and from recordings made on different days or years. This sampling technique mimimized the probablity of incorrect identification. However, when a series of tests was done on smaller, more limited data sets to examine whether the surface codas of an unknown walrus could be distinguished from several previously recorded walruses, the margin for incorrect identification was large. Similar results were obtained when another series of tests was done to determine whether recording date and social context influenced the structure of surface codas enough to cause incorrect identification. Males included in these tests were recorded several times and only the surface codas emitted from the most contrasting behavioral situations were used. Under most circumstances this would not be the case and the chance of incorrect identification should decline. In addition, the tests clearly showed which two males had the most similar surface codas; it may be possible to compare other aspects of their songs to improve the chances of correctly identifying them. Development of better analysis techniques will also help solve this problem.

Two questions are being addressed about surface codas. Is there sufficient individual variation for walruses to recognize other individuals, and is there sufficient individual variation for researchers to use them as individually distinctive vocalizations? The results of the two series of tests do not invalidate the possible use of surface codas as individually distinctive vocalizations from the walruses' perspective, but they do set limits for the reliable use of surface codas as possible individually distinctive vocalizations from the researcher's perspective.

A minimum of 108-131 walruses overwintered in the Penny Strait region of the High Arctic from 1987 to 1989; 24 to 64 of those walruses overwintered at the Dundas Island polynya. The number of walruses in the Penny Strait region over the 3-year period was relatively consistent and was comparable to estimates reported by Davis et al. (1978). This consistency suggests that the size of the overwintering population is being limited by some unknown factor, possibly food availability (Fay 1982). Pacific walruses overwintering in the drifting pack-ice of the Bering Sea are relatively mobile and their densities may be at least two orders of magnitude greater than those recorded at the Dundas Island polynya or in the Fairholme Island area (Fay et al. 1984). It is not known why more walruses overwintered in the polynya in some years than in others, but the pattern of freeze-up in the early winter is probably important in determining the relative proportion of walruses overwintering in the different areas of Penny Strait.

Single males, male herds of variable size, and large herds containing females and calves were observed at the Dundas Polynya and in the Fairholme Island area. Although walruses in the Fairholme Island area were not observed for long enough to confirm if breeding activity was taking place, some of the males had fresh wounds and blood was often seen on the ice at haul-out sites. It is likely that males were fighting to gain access to females and that breeding occurred. At the Dundas Island polynya, it appeared that only one or two large herds composed of females and calves frequented the polynya each year. The other large herds were predominantly composed of young adult males. Significant between-year differences in the number of large herds sighted may be a result of there being more males in the area during some years.

The primary critera determining the distribution of walruses in Penny Strait were the reliable occurrence of open water, thin annual ice, and ice features that allowed the walruses to gain access to water. North of Dundas Island, breathing holes and haul-out sites were located along cracks and pressure ridges, at the edge of a multi-year ice pan, or along the edge of some ridged shoreline ice. In the vicinity of the Dundas Island polynya, breathing holes and haul-out sites were located in areas of thin or rotting ice or along the edge of a multi-year ice pan.

Resightings of branded and distinctively marked males indicated that at least some individuals returned to the same overwintering and breeding areas for two or three consecutive years. One male was sited in 1983 and 1984 and then again in 1987, while other males were not resighted during the study period. No branded walruses were recorded moving between the Fairholme Island and Dundas Island wintering areas. Males identified at the Dundas Island polynya at the start of the field season (February) usually remained in the area until the start of spring break-up (late April); it is likely they overwintered in the area. Males hauled out on the ice may form loose associations during the breeding season; it is possible these associations are an extension of the associations observed between singing and non-singing males swimming around the polynya (Chapter 3). These observations are consistent with the idea that there is some overwintering site fidelity and that movements of walruses are restricted during the winter months. Both of these factors are thought to influence the social organization, breeding behavior and mating system of walruses (Stirling 1983; Boness 1991; Chapter 2).

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Appendix 1. The relationship of social context to the physical structure of surface codas.

WALRUS ID	SOCIAL SITUATION	N	PULSES	TOTDUR (ms)	DUR1 (ms)	PRDUR1 (ms)	DUR2 (ms)	PRDUR2 (ms)	COMMENTS
8903(SC1)	Alone	38		1530 (95)*	1149 (85)	150 (20)			shorter
	Females/calves present	34		1558 (67)	1176 (68)	151 (5)			longer
				p=0.0035	p=0.0108	p=0.0004			
8903(SC2)	Alone	43	10.30 (0.80)**bd	1617 (111) a	1101 (88)	162 (13) ab	515 (42) cd		shortest(4)
	Silent male present	31	10.52 (0.96) ac	1587 (90) bc	1061 (63) ab	146 (9) bd	526 (55) b		(3)
	Females/calves present	50	11.32 (1.48) cd	1682 (148) c	1134 (113) b	159 (16) cd	548 (80) ad		(2)
	Copulation	23	11.83 (1.50) ab	1760 (133) ab	1145 (97) a	149 (5) ac	615 (80) abc		longest(1)
			p=0.0001	p=0.0001	p=0.0023	p=0.0001	0.0001		
8906(SC1)	Alone	17	8.41 (1.62)	1267 (143)	1015 (121)				shorter
	Silent male present	12	10.25 (2.22)	1506 (184)	1201 (165)				longer
			p=0.0285	p=0.0037	p=0.0064				
8906(SC2)	Alone	23	16.35 (1.03)	2225 (158)			1018 (119)		longer
	Silent male present	12	15.17 (1.34)	2059 (187)			913 (121)		shorter
			p=0.0207	p=0.0269			p=0.0328		
8907	Alone	80	14.45 (1.21) a	1670 (172) ab	936 (149) ab	142 (5)		100 (5) b	longest
	Silent male present	7	13.57 (0.54)	1507 (52) a	752 (58) a	144 (4)		98 (3) a	
	Females/calves present	27	13.56 (0.58) a	1457 (73) b	737 (50) b	140 (8)		94 (3) ab	shortest
			p=0.0001	p=0.0001	p=0.0001	p=0.0389			
8908(SC1)	Alone	13	13.62 (0.96)	1898 (118)	1205 (118)				longer
	Silent male present	6	12.33 (1.03)	1667 (140)	984 (145)				shorter
			p=0.0388	p=0.0128	p=0.0116				
8910	Alone	35		1924 (123)	1291 (97)	130 (8)		119 (6)	longer
	Females/calves present	31		1742 (146)	1105 (110)	125 (8)		113 (6)	shorter
				p=0.0001	p=0.0001	p=0.0053		p=0.0020	

* Mean (SD); ** Matching letters indicate significant multiple-pairwise comparisons within an individual and within a particular variable

Appendix 2. The relationship of the intensity of background vocalizations (BKGV) to the structure of surface codas.

WALRUS ID	INTENSITY OF BKGV	N	PULSES	TOTDUR(ms)	DUR1 (ms)	PRDUR1 (ms)	DUR2 (ms)	PRDUR2 (ms)	COMMENTS
8803	Moderately Loud	13			657 (15)	219 (5)			longer
	Loud	8			637 (19)	212 (6)			shorter
					p=0.0444	p=0.0444			
8805(SC1)	None	6				127 (11) a		106 (2) a	(3)
14/04/88	Faint	11				129 (4)		107 (3)	longest (1)
	Loud	13				130 (5)		105 (2)	(2)
	Distant Clatter	6				136 (3) a		104 (2) a	shortest (4)
						p=0.0484		p=0.0389	
8805(SC2)	Faint	15	13.27 (0.88)	1693 (69)	1181 (70)				longer
1988	Moderately Loud	10	12.60 (0.52)	1549 (31)	1051 (35)				shortert
			p=0.0638	p=0.0004	p=0.0008				
8903(SC2)	None/Faint	13			1038 (41)		509 (18)	127 (4)	longer
	Moderately Loud	8			1004 (23)		519 (7)	130 (2)	shorter
					p=0.0339		p=0.0772	p=0.0772	
8904	Faint	12	12.33 (0.61)	1606 (153) b	883 (157) b	151 (7)			
	Moderately Loud	26	12.65 (0.46) a	1647 (127) a	909 (145) a	155 (6)			longest
	Loud	18	11.83 (0.71) a	1485 (112) ab	768 (68) ab	151 (5)			shortest
			p=0.0030	p=0.0005	p=0.0006	p=0.0234			
8906(SC2)	None	5	16.00 (0.71)				1060 (51)		shorter
27/02/89	Loud	4	17.25 (0.50)				1141 (33)		longer
			p=0.0706				p=0.0484		
8907	None	27	15.19 (1.08) a	1758 (161) a	1023 (156) ab				longest
	Faint	25	14.76 (0.60) b	1681 (79)	918 (65) b				
	Moderately Loud	16	13.81 (1.28) ab	1665 (210) a	941 (179) a				shortest
			p=0.0002	p=0.0300	p=0.0059				

WALRUS ID	INTENSITY OF BKGV	N	PULSES	TOTDUR(ms)	DUR1 (ms)	PRDUR1 (ms)	DUR2 (ms)	PRDUR2 (ms)	COMMENTS
8908(SC2)	None/Faint	12	11.25 (1.66)	1581 (254)	1033 (256)	166 (12)			longer
	Moderately Loud	16	9.50 (0.97)	1390 (132)	830 (136)	191 (19)			shorter
			p=0.0036	p=0.0530	p=0.0374	p=0.0025			
8910	None	16	13.88 (1.45)	1647 (137)	1034 (97)	129 (9)	613 (84)	111 (7)	shorter
	Loud	15	15.73 (59)	1844 (67)	1182 (63)	121 (5)	662 (62)	116 (3)	longer
			p=0.0010	p=0.0006	p=0.0008	p=0.0184	p=0.0620	p=0.0115	

*Mean (SD); ** Matching letters indicate significant multiple-pairwise comparisons within an individual and within a variable

Appendix 3. The relationship of recording date to the structure of surface codas.

WALRUS ID	DATE	N	PULSES	TOTDUR (ms)	DUR1 (ms)	PRDUR1 (ms)	DUR2 (ms)	PRDUR2 (ms)	COMMENTS
8903(SC1)	13/02/89	15	10.53 (0.74)*				380 (34)	127 (11)	longer
	21/03/89	12	9.42 (0.52)				377 (7)	126 (2)	shorter
			p=0.0021				p=0.0964	p=0.0964	
8903(SC2)	13/02/89	14	10.86 (1.03) **a	1653 (78) a	1126 (74) a	145 (13) a			longer
	21/03/89	37	9.92 (0.76) a	1547 (42) a	1038 (41) ab	145 (4) b			shorter
	15/04/89	13	10.41 (0.80)	1613 (11) a	1097 (83) b	165 (11) ab			
			p=0.0098	p=0. 0002	p=0.0005	p=0.0001			
8907	07/03/89	15		1458 (79)	764 (45)			97 (3)	shorter
	19/03/89	15		1661 (217)	943 (185)			106 (8)	longer
				p=0.0017	p=0.0122			p=0.0015	
8805(SC1)	19/03/88	12			1048 (115)		791 (97)		shorter
	14/04/88	17			1175 (115)		689 (71)		longer
					p=0.0231		p=0.0150		
8805(SC2)	19/03/88	9	12.57 (0.53)	1558 (27)	1047 (35)				shorter
	14/04/88	16	13.25 (0.86)	1679 (86)	1175 (71)				longer
			p=0.0554	p=0.0025	p=0.0011				
8805(SC2)	27/03/89	22	12.18 (0.66) a	1569 (75) a			489 (47) a	102 (3) a	shortest (4)
	01/04/89	23	12.09 (0.60) bc	1580 (59) b			510 (32)	104 (4)	(3)
	06/04/89	14	12.71 (0.73) c	1612 (76)			513 (32)	104 (9)	(2)
	07/04/89	9	12.89 (0.33) ab	1661 (62) ab			539 (47) a	108 (9) a	longest (1)
			p=0.0022	p=0.0097			p=0.0077	p=0.0446	

* Mean (SD); ** Matching letters indicate significant multiple-pairwise comparisions within an individual and within a variable

Appendix 4. The relationship of location in singing-bout to the structure of surface codas.

WALRUS ID	BOUT LENGTH (hrs)	BOUT PHASE	N	PULSES (ms)	TOTDUR (ms)	DUR1 (ms)	PRDUR1(3)	DUR2 (ms)	PRDUR2 (ms)	COMMENTS
8801	4.5	Beg	15	12.13 (0.83)	1510 (108)		136 (14)			longer
		End	15	10.93 (0.70)	1420 (129)		149 (12)			shorter
				p=0.0024	p=0.0248		p=0.0186			
8802	1.5	Beg	8	15.63 (1.51)	1811 (68)	1153 (85)		658 (58)		longer
		End	9	14.89 (0.93)	1634 (102)	1051 (73)		583 (54)		shorter
				p=0.0508	p=0.0079	p=0.0333		p=0.0158		
8804	2.8	Beg	10		1960 (129)			740 (56)	118 (9)	longer
		End	11		1798 (89)			683 (75)	111 (8)	shorter
					p=0.0123			p=0.0713	0.0873	
88B11	4.5	Beg	10		2177 (109)					longer
		End	10		2066 (138)					shorter
					p=0.0376					
88B44	1.5	Beg	9	11.78 (0.97)	1667 (127)		159 (6)	683 (76)	129 (5)	longer
		End	10	10.80 (1.03)	1562 (122)		154 (6)	574 (80)	122 (7)	shorter
				p=0.0678	p=0.0889		p=0.0761	p=0.0189	p=0.0700	
8805(SC1)	31	Beg (1-4)	19	15.05 (1.18)						(3)
20/04/88		(7-8)	32	14.28 (1.71)						shortest (5)
		(15-16)	19	15.37 (1.12) a						longest (1)
		(20-25)	13	14.46 (1.51)						(2)
		End (28-31)	9	13.67 (1.87) a						(4)
				p=0.0385						
8805(SC2)	31	Beg (1)	18				128 (7) a		107 (3)	(2)
20/03/88		(7-8)	17				132 (11)		108 (5) a	longest (1)
		(13-14)	19				128 (6) b		105 (3) a	(3)
		End (21-24)	6				138 (2) ab		104 (2)	shortest (4)
							p=0.0044		p=0.0216	

WALRUS ID	BOUT LENGTH (hrs)	BOUT PHASE	N	PULSES (ms)	TOTDUR (ms)	DUR1 (ms)	PRDUR1(3)	DUR2 (ms)	PRDUR2 (ms)	COMMENTS
8805(SC1)	7.0	Beg	3	12.67 (0.58)	1654 (7)		139 (1)	629 (8)	105 (1)	shorter
01/04/88		End	10	14.60 (1.58)	1812 (148)		124 (10)	727 (91)	110 (3)	longer
				p=0.0670	p=0.0302		p=0.0296	p=0.0413	p=0.0302	
8901	3.0	Beg	15	13.20 (0.68)	1534 (76)					shorter
		End	16	14.19 (0.66)	1640 (8)					longer
				p=0.0078	p=0.0022					
8903(SC1)	3.5	Beg	4	9.50 (0.58)						shorter
13/02/89		End	13	10.69 (0.63)						longer
				p=0.0236						
8903(SC2)	3.5	Beg	7		1712 (101)	1167 (71)	149 (51)			longer
13/02/89		End	9		1619 (59)	1089 (48)	140 (4)			shorter
					p=0.0590	p=0.0411	p=0.0462			
8903(SC2)	7.5	Beg	10		1558 (40)	1047 (41)				longer
21/03/89		End	8		1523 (23)	1004 (23)				shorter
					p=0.0322	p=0.0187				
8904	1.5	Beg	16	12.75 (0.48)	1657 (75)		158 (5)			shorter
17/02/89		End	8	13.13 (0.64)	1756 (96)		153 (4)			longer
				p=0.0402	p=0.0307		p=0.0582			
8904	1.5	Beg	10				155 (6)			longer
16/03/89		End	10				148 (4)			shorter
							p=0.0198			
8906(SC1)	1.5	Beg	5				135 (3)	237 (44)		shorter
20/02/89		End	7				139 (3)	353 (109)		longer
							p=0.0500	p=0.0668		

WALRUS ID	BOUT LENGTH (hrs)	BOUT PHASE	N	PULSES (ms)	TOTDUR (ms)	DUR1 (ms)	PRDUR1(3)	DUR2 (ms)	PRDUR2 (ms)	COMMENTS
8907	8.5	Beg	20	15.00 (0.73)	1718 (107)	987 (100)	139 (7)			
		Mid	16	15.38 (1.20) a	1788 (179) a	1026 (183) a	145 (2) ab			longest
		End	17	14.59 (0.51) a	1661 (66) a	903 (600) a	142 (3) b			shortest
				p=0.0458	p=0.0268	p=0.0070	p=0.0003			
8908(SC2) 12/02/89	2.0	Beg	13	9.31 (0.95)		815 (147)	196 (12)			shorter
		End	4	10.50 (0.58)		940 (91)	171 (13)			longer
				p=0.0284		p=0.0643	p=0.0643			
8908(SC1) 20/04/89	9.0	Beg	9				147 (15)	648 (64)	133 (10)	longer
		End	12				152 (6)	710 (54)	143 (11)	shorter
							p=0.0486	p=0.0521	p=0.0486	
8910	2.0	Beg	10	13.46 (0.93)	1833 (12)			582 (75)	118 (4)	shortest
		End	10	15.09 (0.94)	1971 (84)			673 (83)	123 (6)	longest
				p=0.0043	p=0.0075			p=0.0193	p=0.0256	
8912	1.5	Beg	14	13.79 (0.58)	1622 (579)	875 (40)				longer
		End	15	13.06 (0.46)	1596 (35)	842 (18)				shorter
				p=0.0039	p=0.0475	p=0.0043				

* Mean (SD); **Matching letters indicate significant multiple-pairwise comparisons within an individual and within a variable

Appendix 5. Relationship of order of emission to the structure of surface codas.

WALRUS ID	ORDER	N	PULSES (ms)	TOTDUR (ms)	DUR1 (ms)	PRDUR1 (ms)	DUR2 (ms)	PRDUR2 (ms)	COMMEMTS
88B11	first	17	15.12 (0.78)	2045 (103)	1265 (98)				shorter
	second	19	15.63 (0.99)	2158 (122)	1341 (101)				longer
			p=0.0742	p=0.0110	p=0.0852				
88B44	first	18			964 (77)	159 (9)			shortest
	second	14			999 (56)	155 (8) a			
	third	7			1032 (111)	169 (21) a			longest
					p=0.0932	p=0.0143			
B02	first	17	14.29 (1.05)	1753 (94)	1107 (88)				shorter
	second	17	15.35 (1.06)	1875 (83)	1197 (63)				longer
			p=0.0116	p=0.0025	p=0.0048				
8906(SC2) 20/02/89	first & second	5					810 (46)	119 (4) a	shortest
	third	7					939 (129)	119 (5) b	longest
	fourth to sixth	5					965 (103)	127 (4) ab	
							p=0.0569	p=0.0340	
8906(SC1) 27/02/89	first	6				127 (15)			shorter
	second	6				141 (4)			longer
						p=0.0302			
8805(SC1) 20/04/88	first	30	14.13 (1.59)	1733 (163) a			699 (89) a	107 (7)	shortest
	second	28	14.57 (1.55)	1815 (174)			763 (105) a	111 (6)	
	third	25	15.12 (1.42)	1853 (173) a			765 (113)	110 (7)	longest
			p=0.0553	p=0.0367			p=0.0244	p=0.0450	
8805(SC1) 1989	First	31	14.39 (1.31) b	1816 (146)			717 (87) b	109 (4)	
	Second	37	14.65 (1.38) a	1840 (158)			723 (78) a	109 (5) a	longest
	Third	8	13.25 (1.17) ab	1723 (158)			647 (63) ab	105 (4) a	shortest
			p=0.0172	p=0.0620			p=0.0135	p=0.0482	

* Mean (SD); ** Matching letters indicate significant multiple-pairwise comparisons within an individual and within a variable

Appendix 6. Relationship of coda song variation to the structure of surface codas.

WALRUS ID	CODA SONG	N	PULSES (ms)	TOTDUR (ms)	DUR1 (ms)	PRDUR1 (ms)	DUR2 (ms)	PRDUR2 (ms)	COMMEMTS
8903(SC1)	typical	21	10.24 (0.83)						shorter
	erratic	9	9.25 (0.50)						longer
			p=0.0448						
8904	typical	6				160 (5)			shorter
	erratic	7				149 (6)			longer
						p=0.0243			
8906	typical	3		1862 (66)			783 (44)		shorter
	long	7		2137 (186)			971 (107)		longer
				p=0.0705			p=0.0486		

*Mean (SD); ** Matching letters indicate significant multiple-pairwise comparisons within an individual and within a variable